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# THE BIOLOGY OF THE RAINBOW TROUT (*Salmo gairdnerii*) IN THE LAKES OF THE ROTORUA DISTRICT, NORTH ISLAND

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*(Received for publication, 21 April 1959)*

## *Summary*

Trout populations were studied in 11 lakes of varied size and environmental characteristics in the Rotorua district. All lakes contained rainbow trout and 2 also contained brown trout. Temperatures varied seasonally between 7° C and 25° C, and the only 2 lakes examined were thermally stratified. The fish were caught mainly with gill-nets of 2 in., 3 in., and 4 in. mesh, the 3 in. net being the most efficient; all nets were most effective at night. All 3 nets were highly selective, their effective length-ranges being 28 to 52 cm, 42 to 50 cm, and 18 to 25 cm respectively.

Growth of fish is rapid although there is some variation between the lakes. Fish reach 25 to 42 cm in the first year and 30 to 56 cm in the second. Most of the fish mature at this age and little further growth occurs. In most lakes the sexes are equally numerous, but excesses of either males or females occur in some lakes. There appears to be a tendency for males to predominate in old stocks and females in young stocks. Population densities of adult fish are generally between 3 and 10 per acre. The age structure varies considerably, the average age being apparently lowest where good spawning streams are available.

The main food of trout of all sizes was the smelt (*Retropinna* sp.); other important foods were bullies (*Gobiomorphus* sp.) and koura (*Paranephrops* sp.) particularly in the larger trout, and insects mainly of terrestrial origin, particularly in the smaller trout. Very little evidence of cannibalism was found, although in a few lakes trout taken in the spawning season contained appreciable numbers of trout eggs.

*Mr Derek Smith was killed in a road accident on July 30th, 1958, while work which he had planned on this topic was still in its early stages. This paper has been prepared for publication by K. Radway Allen from reports that Mr Smith had written dealing with the results obtained up to the end of 1957.

## INTRODUCTION

The lakes in the Rotorua district, just north of the centre of the North Island, support an important trout fishery which in 1952 yielded 536,000 lb of trout out of a total North Island catch of 1,729,000 lb (Allen and Cunningham, 1957). In view of the importance of this fishery it was decided to undertake an investigation of the life history and general biology of trout in these lakes, with the object of developing improved management techniques. Work was begun early in 1956, and the present paper deals with the results up to the end of 1957. By this time the first stage of the planned programme had been largely completed; a survey had been made of most of the lakes in the district to obtain data on population densities, growth rates, and feeding habits.

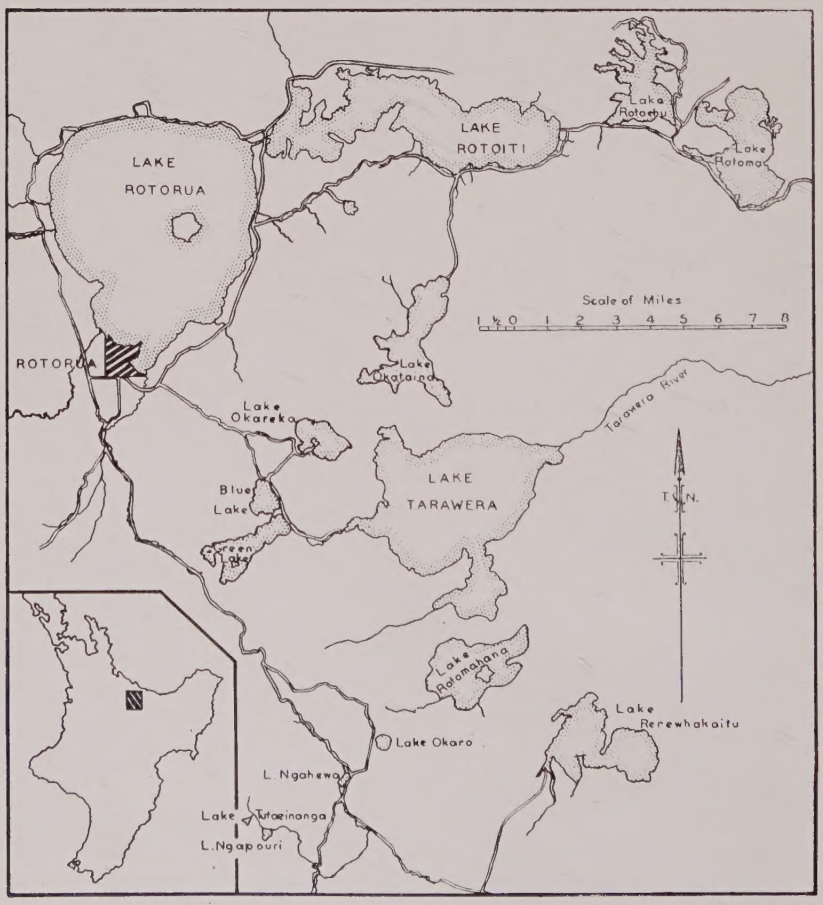


FIG. 1.—Map of the Rotorua lakes.

Trout are not native to New Zealand but were introduced in the second half of the last century because the native freshwater fish were of little sporting or food value. Brown trout (*Salmo trutta*) were first introduced, but they were less successful in the northern half of the North Island than the rainbow trout (*S. gairdnerii*) which was introduced later. The Rotorua lakes contain only rainbow trout, except for Lakes Rotorua and Rotoiti which also contain brown trout.

The Rotorua lakes lie in a fairly compact area (Fig. 1) which has been the scene of much recent volcanic and seismic activity and the lakes have been formed by this activity in a variety of ways; several of them are formed entirely or in part by the craters of volcanic explosions (Grange, 1937). The lakes vary greatly in shape and dimensions, and the main features of those referred to in this paper are summarized in Table 1. A striking feature of these lakes is the frequent absence of any surface overflow, although several lakes are known to have underground outflows. Many are fed only by a few very small tributaries and the unsatisfactory conditions which these provide for the spawning of trout have a considerable effect on the fish populations.

TABLE 1.—Main Feature of the Lakes Studied in Most Detail.

| Lake | Area (acres) | Altitude (ft) | Max. depth (ft) | Shore-line (miles) | Surface outlet | Spawning streams |
|---|---|---|---|---|---|---|
| Ngapouri | 54 | 1565 | 88 | 1·55 | Yes | One, fair |
| Ngahewa | 22 | 1347 | 30 | 0·91 | Yes | One, good |
| Okaro | 80 | 1353 | 52 | 1·48 | No | No |
| Rotokawau | 122 | 1100 | c. 270 | 1·67 | No | No |
| Blue | 370 | 1358 | 84 | 3·1 | No | No |
| Okareka | 790 | 1154 | 132 | 5·5 | No | Two, poor |
| Rotoehu | 1850 | 963 | 38 | 24·7 | No | Several, fair to good |
| Okataina | 2450 | 1014 | 269 | 17·5 | No | Several, poor |
| Rotoma | 2800 | 1035 | 262 | 15·1 | No | Few, poor |
| Rotoiti | 8250 | 913 | 230 | 35·7 | Yes | One good, and via L. Rotorua |
| Rotorua | 17000 | 915 | 84 | 23·5 | Yes | Several, good |

Although fish were taken from all the Rotorua lakes that hold trout, this paper deals with the 11 lakes from which significant samples have been taken. The numbers of fish taken by different methods in each lake are noted in Table 2. The bulk of the fish have been taken in gill-nets. Five lakes were sampled at more or less regular intervals through the year; 2 were sampled in the later winter of 1956 and at the same period in 1957, and the remaining 4 were sampled once only. In all but the 5 lakes that were sampled repeatedly the fish were taken over at least 2 nights; these were usually consecutive but once were 22 days apart (L. Rotoiti).

TABLE 2.—Numbers of Fish Taken by Various Methods from each of the Principal Lakes Studied in this Investigation.

| Lake | Method of Capture | | | | | Total |
|---|---|---|---|---|---|---|
| | Gill Net | Seine Net | Rod | Various | Tributaries and outlets | |
| Ngapouri | | | | | | |
| (adults) | 299 | 7 | 52 | 3 | 65 | 426 |
| (fry) | 0 | 0 | 0 | 0 | 423 | 423 |
| Ngahewa | 134 | 11 | 15 | 0 | 19 | 179 |
| Okaro | 107 | 1 | 6 | 0 | 0 | 114 |
| Rotokawau | 31 | 0 | 0 | 0 | 0 | 31 |
| Blue | 121 | 0 | 0 | 0 | 0 | 121 |
| Okareka | 145 | 0 | 0 | 0 | 20 | 165 |
| Rotoehu | 316 | 3 | 6 | 2 | 0 | 327 |
| Okataina | 162 | 0 | 0 | 0 | 26 | 188 |
| Rotoma | 49 | 7 | 0 | 0 | 0 | 56 |
| Rotoiti | | | | | | |
| (Rainbow) | 68 | 0 | 0 | 0 | 0 | 68 |
| (Brown) | 1 | 0 | 0 | 0 | 0 | 1 |
| Rotorua | | | | | | |
| (Rainbow) | 52 | 0 | 0 | 0 | 0 | 52 |
| (Brown) | 24 | 0 | 0 | 0 | 0 | 24 |
| Total | 1509 | 29 | 79 | 5 | 553 | 2175 |

As far as possible major samples were taken from all lakes during the closed season for angling (June to October inclusive): it was initially assumed that growth in length and changes in feeding habits would be relatively slow, and hence that valid comparisons between stocks could be made even when the samples were taken a few weeks apart. In practice, although changes in length did occur, the data on growth rates obtained from the repeated samples enabled corrections to be derived for the differences in time.

Detailed temperature records were maintained at Lake Ngapouri and Okaro. Maximum-and-minimum thermometers, which were read fortnightly, were installed close to the surface inshore and just off the bottom in 25 m. in Lake Ngapouri and inshore only in Lake Okaro. In the other lakes temperature readings were taken as opportunity occurred. Figure 2 shows the variation in temperature at the surface in Lake Ngapouri during 1957. The readings obtained in the other lake were very similar. Vertical series at 1 m. interval were taken in Lake Ngapouri on 13/2/57 and in Lake Okaro on 31/1/57; both lakes were found to be thermally stratified with the thermoclime between 6 and 11 m. The hypolimnion temperatures were 10·6° C and 10·0° C respectively. On 2/1/58 the thermocline in L. Okataina was found by diving to be at about 20 m. (R. M. Cassie, pers. comm.). A vertical series in Lake Ngapouri on 2/7/57 showed it to be completely mixed with a temperature of 9·0° C. The lowest minimum temperature recorded on the bottom was 6·7° C.

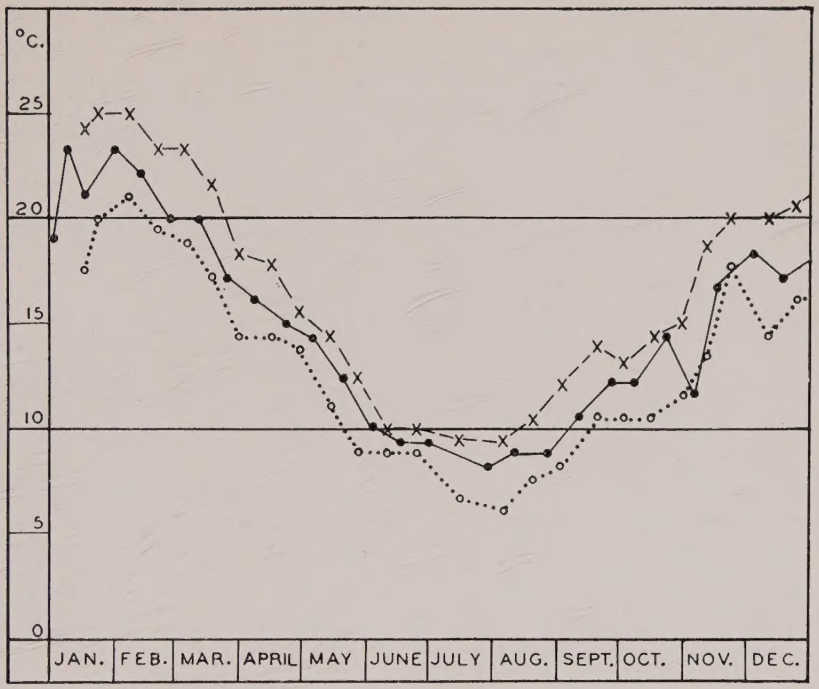


FIG. 2.—Temperature readings taken at the surface in Lake Ngapouri in 1957. The upper and lower lines represent the maximum and minimum temperatures for the 2 weeks centred on each date; the middle line is the actual temperature at the time of reading.

## THE EFFICIENCY AND SELECTIVITY OF THE GILL-NETS

As Table 2 shows, the great majority of the fish taken were caught with gill-nets. Three nets were used to obtain most of the samples. These were:

*Net 1* Linen, 4 in. stretched mesh, 86 yards long, 6 ft deep.
*Net 2* Nylon, 3 in. stretched mesh, 67 yards long, 8 ft deep.
*Net 3* Nylon, 2 in. stretched mesh, 67 yards long, 8 ft deep.

Except in the first few months of the work, all 3 nets were in use on each occasion, and they were normally set with one end on shore and at right-angles to it.

To obtain from the catches data regarding the density and composition of fish populations of the lakes it is necessary to examine the efficiency and selectivity of the nets.

### *Efficiency*

The nets show considerable differences in their rates of catch under comparable conditions; they also differ in their relative effectiveness

by day and by night. Up to February 1957, the nets were usually examined at intervals of a few hours so that it was possible to distinguish between day and night catches; the results are compared in Table 3. Where a set was made partly in daylight and partly in darkness the catch has been divided in proportion to the day and night catches.

TABLE 3.—Comparison of Day and Night Catches by each Net in Several Lakes.

| Net No. | | | Lake | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Ngapouri | Ngahewa | Okaro | Blue | Rotoehu | Total |
| 1 | Day | Hr | 35 | 20 | 36 | 45 | 44 | 180 |
| | | Fish/hr | 0·49 | 0·15 | 0·03 | 0·20 | 0·25 | 0·23 |
| | Night | Hr | 42 | 17 | 40 | 48 | 22 | 169 |
| | | Fish/hr | 0·36 | 0·23 | 0·02 | 0·40 | 0·64 | 0·31 |
| 2 | Day | Hr | 20 | 19 | 36 | 45 | 35 | 155 |
| | | Fish/hr | 0·05 | 0·79 | 0·06 | 0·02 | 0·11 | 0·15 |
| | Night | Hr | 38 | 16 | 40 | 45 | 22 | 164 |
| | | Fish/hr | 2·00 | 1·93 | 0·07 | 0·90 | 2·21 | 1·23 |
| 3 | Day | Hr | 12 | 19 | 37 | — | 21 | 89 |
| | | Fish/hr | 0·08 | 0·37 | 0 | — | 0 | 0·09 |
| | Night | Hr | 34 | 26 | 40 | — | 22 | 122 |
| | | Fish/hr | 0·47 | 0·89 | 0·02 | — | 0·32 | 0·39 |

Except for net 1 on L. Ngapouri and L. Okaro all nets fished more efficiently by night. In the clearest lakes (Blue L. and L. Rotoehu) nets 2 and 3 fished very poorly by day, and this was also the case in L. Ngapouri which is fairly turbid. In L. Ngahewa, which is very turbid, the day catch was, by contrast, fairly high.

Table 4 gives the catches obtained in 2 lakes by setting nets for 4 nights. In Blue L. the nights were successive but in L. Ngapouri there were intervals of about a month between the second and third, and the third and fourth nights. The constancy of the catch in each lake is noteworthy. In L. Ngapouri it is even more significant when the first 3 nights only are considered. During each of these nights, nets 2 and 3 were placed on opposite shores of the lake and were moved during the night so that each net fished for half the night in each position. They then fished each position for the same total length of time. On the fourth night the nets were set in other positions and not moved, and this may account for the changes in the relative catch. In Blue L. the net was fished in the same position over the four nights.

The full catches of each net since they were first used are shown in Table 5. It is clear that net 2, the 3 in. mesh nylon net, is by far the most efficient net, taking half as many fish again as the other two nets combined. The validity of this conclusion could be affected if the nets had been fished for relatively different periods under different conditions but in practice all 3 nets were usually fished simultaneously.

TABLE 4.—Comparison of Successive Catches by the Same Net in the Same Lake.

| Lake | Net | 1 Date | 1 Catch | 2 Date | 2 Catch | 3 Date | 3 Catch | 4 Date | 4 Catch |
|---|---|---|---|---|---|---|---|---|---|
| Ngapouri | 2 | 16/10/56 | 14 | 17/10/56 | 12 | 23/11/56 | 12 | 20/12/56 | 18 |
| | 3 | 16/10/56 | 5 | 17/10/56 | 6 | 23/11/56 | 5 | 20/12/56 | 0 |
| Blue | 2 | 23/8/56 | 13 | 24/8/56 | 12 | 25/8/56 | 9 | 26/8/56 | 9 |

The only important exceptions were in L. Okataina in June and July 1957, when net 1 was not used and in L. Ngapouri, Blue Lake, and L. Okareka in June to September 1956, when net 3 was not fished. These exceptions are clearly not enough to account for the difference in catches.

### *Selectivity*

Figure 3 shows the size distribution of the combined catch from all lakes by each net. Net 2 is the least selective and between 28 and 52 cm it does not appear to select at all, or if it does then it is an even and gradual selection and would not account for the discontinuities or the irregularities of the component samples. Net 1 is more selective than net 2 but it takes fish effectively between 42 cm and 50 cm; net 3 is highly selective, taking the bulk of its fish only between 18 and 25 cm. The lower limits are certainly not due to absence of smaller fish; the nets were fished throughout the year and young fish in all sizes must have been present; but only 6 fish under 18 cm were taken. It is possible that the young fish were not inshore when the nets were set, but there is no evidence of this.

The curves for nets 2 and 3 are bimodal with peaks at about 28 and 49 cm and 20 and 52 cm respectively; this fact, together with the wide size range of the fish caught by these nets, suggests that two catching mechanisms exist; enmeshing, where the fish can get its head but not its shoulders through the mesh; and entangling, where the fish is originally lightly caught by a jaw or fin but becomes well wrapped in the net in its struggles to free itself. Fish of sizes considerably greater than the enmeshing size can apparently become entangled, as the peak for net 3 between 44 and 58 cm shows, but the evidence is not yet sufficient to enable the efficiencies of the two processes to be compared. Net 1 has only a single peak at about 45 cm and it may be that for this large-meshed net the enmeshing size range reaches well up towards the maximum size of fish in these lakes.

The combined distribution for the 3 nets as shown in Fig. 3 reflects the structure of the

TABLE 5.—Total Catches by each Net, and Rates of Catch, in the Principal Lakes.

| Lake | Net-hrs fished | Net 1 | | Net 2 | | Net 3 | | Total | |
|---|---|---|---|---|---|---|---|---|---|
| | | No. | Fish/hr | No. | Fish/hr | No. | Fish/hr | No. | Fish/hr |
| Ngapouri | 387 | 28 | 0·22 | 199 | 1·55 | 42 | 0·33 | 269 | 0·70 |
| Ngahewa | 114 | 6 | 0·15 | 61 | 1·8 | 49 | 1·2 | 116 | 1·00 |
| Okaro | 291 | 41 | 0·39 | 75 | 0·81 | 17 | 0·18 | 133 | 0·44 |
| Rotoehu | 159 | 63 | 1·19 | 194 | 3·66 | 55 | 1·04 | 312 | 1·84 |
| Okataina | 227 | 31 | 0·53 | 97 | 1·15 | 39 | 0·46 | 167 | 0·74 |
| Rotokawau | 60 | 11 | 0·55 | 13 | 0·65 | 7 | 0·35 | 31 | 0·52 |
| Blue | 240 | 25 | 0·26 | 76 | 0·79 | 8 | 0·17 | 108 | 0·45 |
| Okareka | 99 | 19 | 0·86 | 38 | 0·86 | 10 | 0·30 | 67 | 0·68 |
| Rotoma | 72 | 20 | 0·83 | 22 | 0·92 | 6 | 0·25 | 48 | 0·67 |
| Rotoiti | 75 | 36 | 1·44 | 26 | 1·04 | 9 | 0·36 | 71 | 0·91 |
| Rotorua | 99 | 22 | 0·67 | 42 | 1·27 | 8 | 0·24 | 72 | 0·73 |
| Total | 1823 | 302 | 0·50 | 842 | 1·32 | 250 | 0·43 | 1394 | 0·69 |

fish populations as modified by the effectiveness of the nets. It clearly takes its general form from net 2; net 3 extends the lower range although there is a sharp gap at about 22 cm. Net 1 fills to some extent the gap between the peaks of net 2 and also reinforces the second peak, so the composite curve shows a preponderance of large fish.

As will be shown later, individual catches were nearly always bimodal, and the size of fish in the larger group did not vary seasonally to a significant extent. This group was therefore represented in all catches and by the frequency of its appearance produces the peaks about 45 to 55 cm in all the curves. The fish in the smaller size-group were growing steadily during the year and therefore would not show separate peaks when samples taken throughout the year are combined. Combination of samples taken from several lakes with slightly different growth rates would further obscure the separate peaks.

It therefore appears that the variations in the samples of fish over 28 cm indicate approximately the size distributions of the populations. Below 28 cm selectivity of the nets causes underestimation of the populations, and below 18 cm the samples are meaningless.

## GROWTH, MATURITY, AND POPULATION

### *Methods*

This part deals with the size of the fish in the lakes, their age and growth, their maturity and sex ratios, and the size and structure of the populations. Each lake will be discussed in turn. The data for comparative size were obtained mainly during the close season (i.e. between June and October) and the length distributions from each of the major samples at this time are shown in Table 6. The bimodal nature of the distributions, with modes corresponding to younger and older fish, is marked in almost all cases and in Table 7 the range and medians of these two groups are shown. The median rather than the mean has

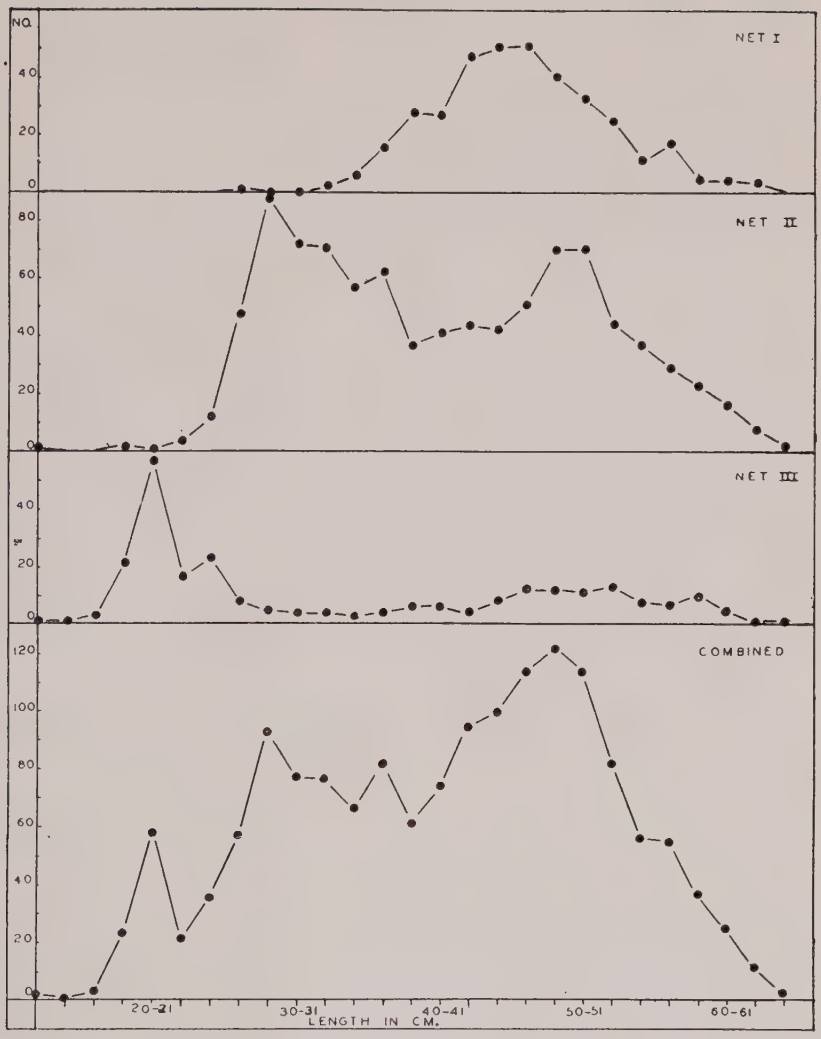


FIG. 3.—Size distribution of fish caught in each of the gill-nets used, and in the three nets combined. Net I—4 in. mesh, linen; net II—3 in. mesh, nylon; net III—2 in. mesh, nylon.

been chosen as being less affected by extreme values in samples, by net sampling errors, and by difficulties in separating the two parts of the distribution. Each value for the range and median has been taken either from a sample taken in August, or by extrapolation where necessary from samples taken as close to August as possible.

TABLE 6.—Size Distribution of Fish Taken in Gill-Nets in the Principal Lakes.

| Lake | Length (cm) | | | | | | | | | | | | | | | | | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Less than 20 | 20–21 | 22–23 | 24–25 | 26–27 | 28–29 | 30–31 | 32–33 | 34–35 | 36–37 | 38–39 | 40–41 | 42–43 | 44–45 | 46–47 | 48–49 | 50–51 | 52–53 | 54–55 | 56–57 | 58–59 | 60–61 | 62– | | |
| Ngapouri | 3 | 7 | 3 | 5 | 22 | 24 | 16 | 8 | 3 | 1 | 3 | 5 | 2 | 6 | 4 | 6 | 3 | 4 | 1 | 1 | 1 | | | | 128 |
| Ngahewa | 13 | 20 | 6 | 9 | 4 | 7 | 13 | 16 | 11 | 18 | 6 | 3 | 5 | 2 | 1 | | | | | | | | | | 134 |
| Okaro | | 3 | | | | 1 | | 3 | | 3 | 6 | 20 | 31 | 26 | 12 | 6 | 1 | | | | | | | | 112 |
| Rotokawau | | | | | | | | | | | | | | 2 | 6 | 6 | 9 | 7 | 1 | | | | | | 31 |
| Blue | 1 | | 1 | 1 | 2 | 8 | 6 | 10 | 6 | 2 | 1 | 3 | 18 | 17 | 15 | 13 | 10 | 6 | | | | | | | 120 |
| Okareka | | | 1 | | | 3 | 2 | 3 | 2 | 3 | | 1 | 1 | 8 | 16 | 25 | 35 | 23 | 12 | 8 | 3 | 1 | | | 147 |
| Rotoehu | 2 | 15 | 2 | 12 | 15 | 28 | 16 | 14 | 11 | 12 | 14 | 11 | 7 | 7 | 15 | 12 | 13 | 18 | 11 | 1 | | | | | 236 |
| Okataina | 1 | 5 | 2 | 2 | 3 | 5 | 1 | 4 | 10 | 6 | 4 | 4 | 4 | 3 | | 1 | 4 | 7 | 14 | 26 | 21 | 19 | 12/2 | | 158 |
| Rotoma | | 1 | 1 | | | | 2 | | 4 | 4 | 4 | | | | | 2 | 4 | 1 | 9 | 10 | 10 | 3 | 1 | | 56 |
| Rotoiti | 1 | 1 | | | | 2 | 2 | | 4 | 4 | 8 | 9 | 8 | 7 | 2 | 3 | 4 | 2 | 4 | 4 | 1 | 1 | 1 | | 68 |
| Rotorua (Rainbow) | | | | 1 | 1 | 2 | 4 | 5 | 5 | 6 | 4 | 2 | 2 | 4 | 6 | 5 | 4 | | | | 1 | | | | 52 |
| Rotorua (Brown) | | | | | | | | | | | 2 | 1 | 3 | 1 | 3 | | | 4 | 3 | 2 | 2 | 2 | 1 | | 24 |

### GROWTH

Growth was estimated in three ways. Firstly, in L. Ngapouri and L. Okaro it was estimated from the return of tagged fish. Fish were measured to the nearest mm and the maximum error of measurement varied from ± 0·2 cm in fish of 10 to 12 cm to ± 0·5 cm in fish of 50 cm or over. Providing it is true to assume that tagged fish are otherwise normal and grow at the same rate as the rest of the population, the values from these results give the most accurate measure of growth. Tagged fish returned by anglers have not been included since the accuracy of the measurements was uncertain.

Growth was also estimated from the change in length with time of the different size groups when repeated samples were taken. The growth in L. Ngapouri, L. Rotoehu, and L. Okataina was estimated in this way. With large samples of fish this method should also give an accurate estimate of growth.

The third estimation of growth was from the difference between the peaks in a polymodal distribution. This estimate is only valid if the growth is the same from year to year since two year-classes are com-

TABLE 7.—The Size Ranges and Approximate Medians of Fish in the Younger and Older Age Groups Taken in the Principal Lakes. The Lengths Adjusted to August.

| Lake | Younger group | | Older group | |
|---|---|---|---|---|
| | Range (cm) | Median (cm) | Range (cm) | Median (cm) |
| Ngapouri | (18)-29 | 26-27 | 40-53 | 46-47 |
| Ngahewa | (17)-28 | 24-25 | — | 29-30 |
| Okaro | — | — | 36-51 | 42-43 |
| Rotokawau | — | — | 44-55 | 50-51 |
| Blue (1956) | 26-39 | 30-31 | 40-53 | 44-45 |
| Blue (1957) | 22-37 | 32-33 | 42-53 | 48-49 |
| Okareka (1956) | (30-37) | (33-34) | 44-61 | 50-51 |
| Okareka (1957) | — | (31-32) | 44-59 | 52-53 |
| Rotoehu | 24-33 | 28-29 | 38-55 | 48-49 |
| Okataina | 25-42 | 35 | 50-65 | 57-58 |
| Rotoma | (20-38) | 35-36 | 48-63 | 56-57 |
| Rotoiti | 28-47 | 40-41 | 46-63 | 54-55 |
| Rotorua (Rainbow) | 24-42 | 34-35 | 43-51 | 46-47 |
| Rotorua (Brown) | 38-47 | 42-43 | 52-63 | 55-56 |

Figures in parentheses are derived from very small numbers of fish, or, in the case of the younger fish in Lakes Ngapouri and Ngahewa, imply failure of the nets used to sample the lower end of the size-range adequately.

pared instead of one year-class being followed through the year. The estimates of growth by this method can be derived from Table 7. This method may be subject to serious errors if the growth rate varies from year to year, but it is clear from comparisons with the results of the repeated samples that in these lakes this method will give a general and reasonable idea of the growth, which is of value in a preliminary study.

### AGE

Age determination in these samples has been done primarily by extrapolation of the growth curves back to fry length (about 2·5 cm) using the repeated samples (L. Ngapouri, L. Rotoehu, and L. Okataina) and depriving the age of fish in the other lakes by analogy. Comparison of the size of introduced tagged fish of known age with that of the native trout in L. Ngapouri and L. Okaro has helped in these lakes and given a lot of information on the age structure of the group of larger fish.

### POPULATION

Rough population estimates can be made from the return of tagged fish in L. Ngapouri and L. Okaro and the relative population of other lakes estimated from these using the catch/gill-net/hour (Table 8)

TABLE 8.—Mean Rates of Catch of Fish of 2 Years and Older by Gill-Nets in the Months May to November in the Various Lakes.

| Lake | No. of Fish | Net-Hrs | Fish/Hr |
|---|---|---|---|
| Ngapouri | 50 | 210 | 0·24 |
| Ngahewa | 11 | 63 | 0·18 |
| Okaro | 122 | 210 | 0·58 |
| Rotokawau | 31 | 60 | 0·52 |
| Blue | 30 | 144 | 0·21 |
| Okareka | 41 | 88 | 0·47 |
| Rotoehu | 90 | 99 | 0·91 |
| Okataina | 105 | 85 | 1·23 |
| Rotoma | 32 | 72 | 0·44 |
| Rotoiti | 23 | 75 | 0·31 |
| Rotorua (Rainbow) | 22 | 99 | 0·22 |
| Rotorua (Brown) | 24 | 99 | 0·24 |

under fairly constant conditions. The present data are somewhat scanty, particularly for the second method, but very approximate estimates of the populations of the different lakes may be made. The use for this purpose of samples taken only between May and November should reduce errors due to the seasonal variation in the availability of fish. Owing to the poor return of young fish estimates are derived only for the older fish.

As the efficiency of the gill-nets, which were the principal means of capture, decreased rapidly for fish below 30 cm in length the population estimates refer only to fish of this size and larger. Except in L. Ngahewa the part of the population estimated would include all the mature fish of 2 years or more and a variable proportion of the immature 1-year-old fish; this proportion would be high in lakes where growth is rapid (e.g. L. Okataina and L. Rotoiti) and low where growth is slower (e.g. L. Ngapouri and L. Rotoehu). In L. Ngahewa, where growth and ultimate size are particularly low, the population estimated does not include even all the mature fish.

The more serious errors are derived from three sources.

(i) Variation in the efficiency of the nets due to (a) selectivity of different nets, (b) the place of setting, (c) concentrations of fish (for this reason nets have not been set at stream mouths except in L. Okaro and L. Ngapouri), (d) moonlight, (e) weather and (f) clarity of the water. All these factors are of unknown or doubtful importance.

(ii) The proportion of fish stocks in the lake at the time of netting. Lakes such as L. Rotorua with many tributaries would have a considerable number of fish in the streams at the time of sampling, while in lakes such as Rotoma and Okataina only a very small proportion of the stock can be out of the lake at any one time.

(iii) The proportion of the fish stocks available for capture by the methods used. At least in large lakes the proportion of

the stock available for capture—in other words liable to swim into the nets during the set—is limited to those inhabiting the littoral region at that time. Fish away from the shores are, at least temporarily, immune from capture. There are at present few data as to the distribution of trout between the open water and the littoral region of these lakes. In this paper the population estimates have been derived both from calculations of fish per acre and of fish per mile of shoreline; no account can be taken of the probability that the population is influenced by a function of both the area and shoreline since no estimate of such a function is yet possible.

In the study of sex ratios, only fish which were sexed by dissection or by the emission of eggs or milt were classified. Fish not so identified are listed as "doubtful"; inevitably these unclassified fish will include a larger proportion of immature fish than of mature but, as can be seen from Fig. 7, their proportion of the stocks, and hence the error, is small. The maturity of the fish was determined from the condition of the gonads and "mature" fish include fish obviously maturing for the next spawning, spawning fish and spent fish. On the whole few fish were taken between November and May except in L. Ngapouri and L. Ngahewa and hence the difficulty of classifying fish showing only the beginnings of maturation rarely arose. Ocasionally some difficulty was found in deciding whether a fish was spent or immature especially some time after spawning; such fish were also listed as "doubtful".

The samples have been split into age groups according to the distributions in Fig. 7. It is believed that these age groups correspond to 1-year-olds (0 + to 1 +) and 2-year-olds and over.

## RESULTS

### *Lake Ngapouri*

#### SIZE OF FISH

The samples from L. Ngapouri were taken at 5-weekly intervals throughout 1957. The August sample is too small to draw fair conclusions from and so the values given for size in Table 7 were from the combined June to October samples. There is little growth among the larger fish at this time so that the mode of this group (46 to 47 cm) is fairly reliable. There is marked growth in the younger fish, however, and the median of the August sample alone (26 to 27 cm) probably gives a fairly reliable indication of the actual median at that time even though the distribution of this group is truncated below 22 cm owing to gill-net selectivity.

#### GROWTH AND AGE

*Lake*

Figure 4 shows the returns of tagged fish to the end of 1957. Several groups of tagged fish are present; hatchery-reared yearlings placed in the lake on 3/11/56; L. Ngapouri fish taken by gill-nets, seine nets,

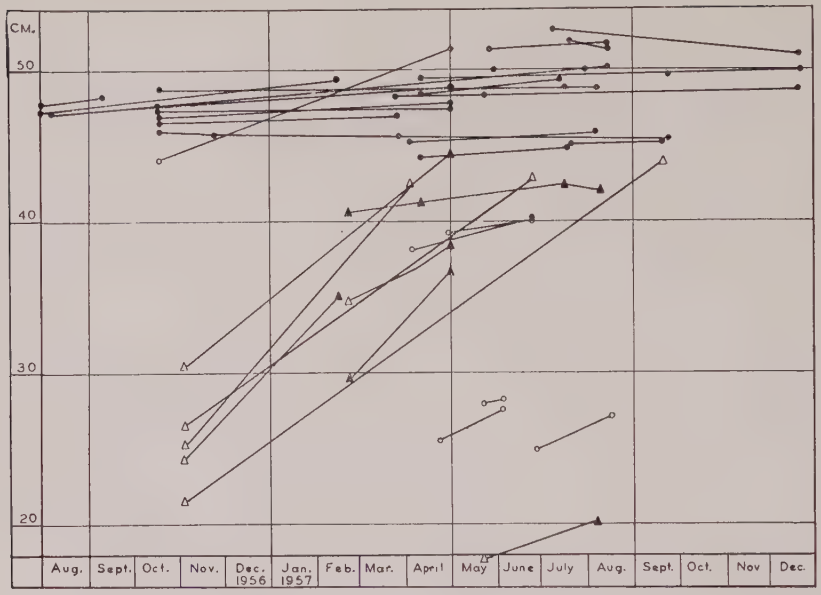


FIG. 4.—Growth of tagged fish in Lake Ngapouri. Circles represent fish reared in the lake, and triangles introduced fish; black and white symbols are mature and immature fish respectively.

or rod; and fish caught by seine or rod in L. Ngahewa and transferred. A summary of fish tagged before 1/7/57 and of recaptures up to 31/12/57 is given in Table 9. It appears that fish less than 39 cm when tagged have a lower chance of recapture than larger fish, possibly on account of a lower survival rate. The numbers of fish are, however, too small to lead to definite conclusions.

A definite growth pattern emerges. Of the older fish (over 40 cm) only 1 grew significantly and this fish, tagged on 16/10/56 was the only fish in the group which was immature when tagged. All the

TABLE 9.—Percentage of Recapture of Tagged Fish Released in L. Ngapouri on or before 1st July 1957, Subdivided According to Their Origin.

| Origin | Hatchery | | Ngahewa | | Ngapouri Gill-Net | | Ngapouri Seine | | Ngapouri Rod | |
|---|---|---|---|---|---|---|---|---|---|---|
| Length when released (cm) | Over 39 | Under 39 | Over 39 | Under 39 | Over 39 | Under 39 | Over 39 | Under 39 | Over 39 | Under 39 |
| No. Tagged | — | 36 | 1 | 23 | 26 | 11 | 5 | 1 | 15 | 14 |
| No. Recaptured | — | 5 | 1 | 4 | 11 | 0 | 4 | 1 | 4 | 3 |
| % Recaptured | — | 14 | 100 | 17 | 42 | 0 | 80 | 100 | 27 | 21 |
| Total % | 14 | | 21 | | 30 | | 83 | | 24 | |

others grew little or not at all. By contrast the young fish both from the hatchery and from L. Ngapouri itself grew considerably. Taking the hatchery and L. Ngapouri fish together the probable growth between November and May is about 10 to 14 cm or 1·5 to 2·0 cm a month.

The growth of the fish transferred from L. Ngahewa is interesting; those transferred in February grew in inverse proportion to their size, although all three were maturing males. Similarly, the one transferred in May, although a maturing male, grew only a little slower than the hatchery and L. Ngapouri immature fish. The continued rapid growth of these fish, although they were maturing, implies that they tended to catch up with the Ngapouri fish because of their originally smaller size, or else that the check in growth of mature fish only happens after they are fully mature.

The second method of studying the growth of fish in L. Ngapouri is illustrated by Fig. 5 which shows the samples taken since September

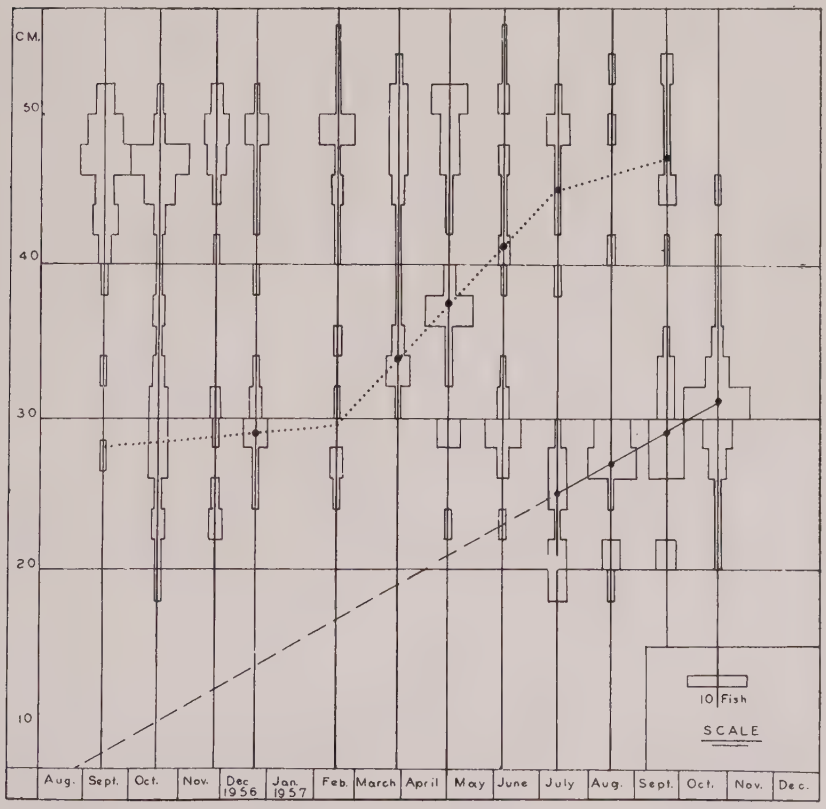


FIG. 5.—Size distributions of successive samples of fish taken in Lake Ngapouri between September 1956 and October 1957. The broken lines show suggested growth curve for two of the principal groups.

1956 plotted for length and time. The width of the figures is proportional to the number of fish in the appropriate 2 cm classes, the dots representing the medians of each group.

The younger size group in July to October 1957, shows a remarkably even growth at an approximate rate of 2 cm every 5 weeks. The July and also to a lesser extent the August samples probably fail to represent the smaller fish of this group in the population (i.e. fish below 20 cm) owing to net selection, and the medians of these samples are probably higher than the true values of the population; hence the true growth rate up to August and possibly up to September, may be underestimated.

If the growth rate of the younger group is taken at 2 cm every 5 weeks and is extrapolated backwards to August 1956 (the broken line on the graph) it crosses the ordinate at 6 cm. Growth in length of the fish in the youngest stages is likely to be the same as, or greater than, that in the older, and the fish of 25 to 31 cm in July to October are therefore probably not more than 1 year old. It will be shown subsequently that the growth of tagged fish in L. Okaro leads to a similar conclusion, and so do the changes in the repeated samples from L. Rotoehu and L. Okataina.

The pattern of growth of the small-medium group from October 1956, to June 1957, is much less regular but seems to follow the course indicated by the dotted line. This suggests that growth was very slow during October to February but was relatively fast from February to July. While the period of slow growth corresponds roughly with the period of highest temperatures, it tends to precede it, since mean temperatures in the lake were above 20° C from about the beginning of January to mid-March and maxima of 25° C or above occurred from the end of January to early March. The growth of these fish is less certain after July 1957, but appears to level out. The results for the previous year-class from September to December 1956, suggest that they grew little if at all in this period.

The results shown in Fig. 5 indicate that the growth in the first year is hence of the order of 25 cm (i.e. from a length at hatching of 2·5 cm to a final length of 27 cm) while that in the second year is about 19 cm (27 to 46 cm).

Both the growth of the tagged fish and the merging of the intermediate group of April to May 1957, in Fig. 5, into the larger group by September suggest strongly that the larger and older fish at any one time are in fact a composite group and not of the same age. They probably include 2- and 3-year-olds as well as some older fish: the exact composition will have to wait upon further work.

There is one group of fish that fail to fit in with this suggested growth rate: these comprise the two samples in May and June 1957, centred at 29 cm and consisting wholly of immature fish. The May sample although compact is small—only 4 fish—but the June sample cannot be ignored. Even if its sudden appearance and disappearance in the samples was due to chance effects it is necessary to account for the presence in the lake of fish so different from the normal size

distribution. Further work is needed to provide the explanation but they could be fish which spent some time in either inlet or outlet creeks before entering the lake; in this case they would be the same age as the next larger group of fish but slightly stunted.

*Inlet Creek*

The first emergence of the fry from the gravel in 1957 occurred between 5 and 19 September. Samples of fry were measured intermittently thereafter until the end of December. The results are shown in Fig. 6. The line BB that has been drawn through the medians of most of the later groups indicates the rate at which the average size of the fry in the creek increases. As, however, fry were moving down into the lake throughout the period, this line would give an underestimate of the actual growth rate. On the other hand the line AA, that joins the largest fry taken in the December collections with the earliest probable hatching date, indicates the growth rate attained by at least some of the fastest growing fry. The growth rate of most of the fry therefore probably lies somewhere between the extremes indicated by those lines, or between 1·0 and 2·0 cm per month.

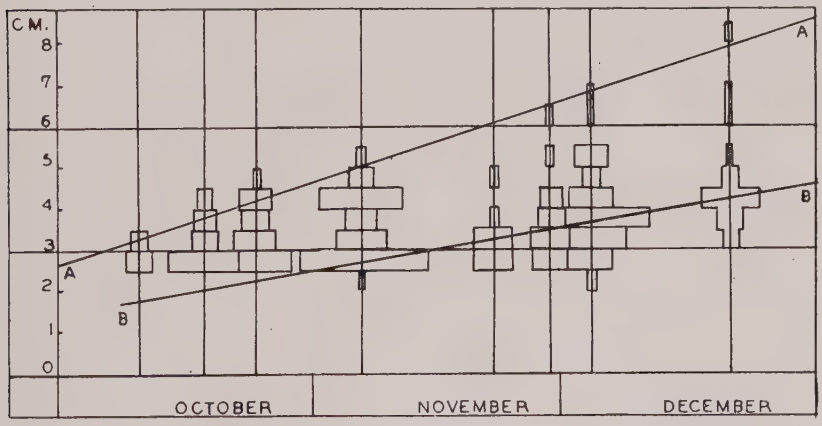


FIG. 6.—Size distributions of successive samples of fry taken in the Lake Ngapouri inlet creek in October to December 1957.

POPULATION

The population of L. Ngapouri can be roughly estimated from the returns of the tagged fish referred to in the previous section. Five sets of data are available; from the regular gill-nettings in April, June, and July, from rod-caught fish in April, and from spawning fish caught in the tributary in July. If these data are combined using the method of least squares (De Lury, 1958) these yield an estimate of 334 fish with 95% confidence limits of 228 and 624. To avoid recruitment errors this estimate is based on, and refers only to, fish of 30 cm or more;

TABLE 10.—The Sex Distribution and Distribution of Mature and Immature Fish in L. Ngapouri.

| Period | Size of Fish (cm) | Mature ♂ | Mature ♀ | Immature ♂ | Immature ♀ | Unclassified | Total ♂ | Total ♀ | Full total |
|---|---|---|---|---|---|---|---|---|---|
| Sept.-Dec. 1956 | > 36 | 24 | 27 | 7 | 2 | 12 | 31 | 29 | 60 |
| | < 36 | — | — | 6 | 16 | 10 | 6 | 16 | 22 |
| | Total | 24 | 27 | 13 | 18 | 22 | 37 | 45 | 82 |
| | % | 29 | 33 | 16 | 22 | — | 45 | 55 | — |
| Feb.-May 1957 | > 40 | 19 | 24 | 0 | 0 | — | 19 | 24 | 43 |
| | < 40 | 2 | 4 | 9 | 16 | — | 11 | 20 | 31 |
| | Total | 21 | 28 | 9 | 16 | — | 30 | 44 | 74 |
| | % | 28 | 38 | 12 | 22 | — | 41 | 59 | — |
| June-Oct. 1957 | >38 | 11 | 11 | 3 | 5 | 2 | 14 | 16 | 30 |
| | < 38 | 0 | 0 | 36 | 49 | 5 | 36 | 49 | 85 |
| | Total | 11 | 11 | 39 | 54 | 7 | 50 | 65 | 115 |
| | % | 10 | 10 | 34 | 46 | — | 43 | 57 | — |
| All | Old | 54 | 62 | 10 | 7 | 14 | 64 | 69 | 133 |
| | Young | 2 | 4 | 51 | 81 | 15 | 53 | 85 | 138 |
| | Total | 56 | 66 | 61 | 88 | 29 | 117 | 154 | 271 |
| | % | 21 | 24 | 23 | 32 | — | 43 | 57 | — |

fish of the 1956 year-class are therefore excluded. Errors due to differences in the method by which the various samples were taken and to mortality in the population as a whole appear to be negligible in comparison with the sampling errors. Errors due to deaths of tagged fish at a greater rate than those of untagged fish between the time of tagging and that of sampling are possible and could be significant. An arbitrary correction has been made on the assumption that this mortality amounts to one-third. The corrected estimate of the number of fish of 30 cm or more then becomes 223 with limits 152 to 416.

Figure 5 shows that there has been a marked change in the composition of the stock during the year. The older group in September and October 1956, has dwindled to a trace in October 1957, and this may be due, at least in part, to the abnormally large number of fish removed by nets and rods. The lack of change in the rate of catch of the gill-nets indicates that the total population has changed little. This suggests that the recruitment to the population within the catchable size range from the 1956 year-class approximately balanced the losses in the older year-classes during the year. The 1956 year-class appears to have been considerably stronger than its immediate predecessors.

### SEX RATIOS AND MATURITY

The distribution of the sexes in fish of the larger and smaller groups is shown in Table 10. The females predominate in the final total and this is just significant. This is a persistent trend and is shown by the figures for the three different periods through the year. The males were, however, relatively more numerous among the larger fish (48%) than among the smaller (38%).

Overall only 4% of the young fish were mature while 13% of the older fish were immature. The distribution of mature fish within the groups shows no strong trends: most of the young mature fish were slightly larger than the immature. The immature fish among the larger group fell either in the centre or towards the smaller fish.

## *Lake Ngahewa*

The size distributions of the samples from this and the remaining lakes are shown in Fig. 7 and the principal features of the populations are summarized in Table 11.

The group centred round 20 to 26 cm in May 1957, probably became the 26 to 35 cm group in November. This would represent a growth rate of 7 to 10 cm in 6 months and would suggest that these fish were yearlings. The fish forming the larger group in May had either died out after spawning or were not caught by the nets.

The predominance of females is highly significant in both young and old fish.

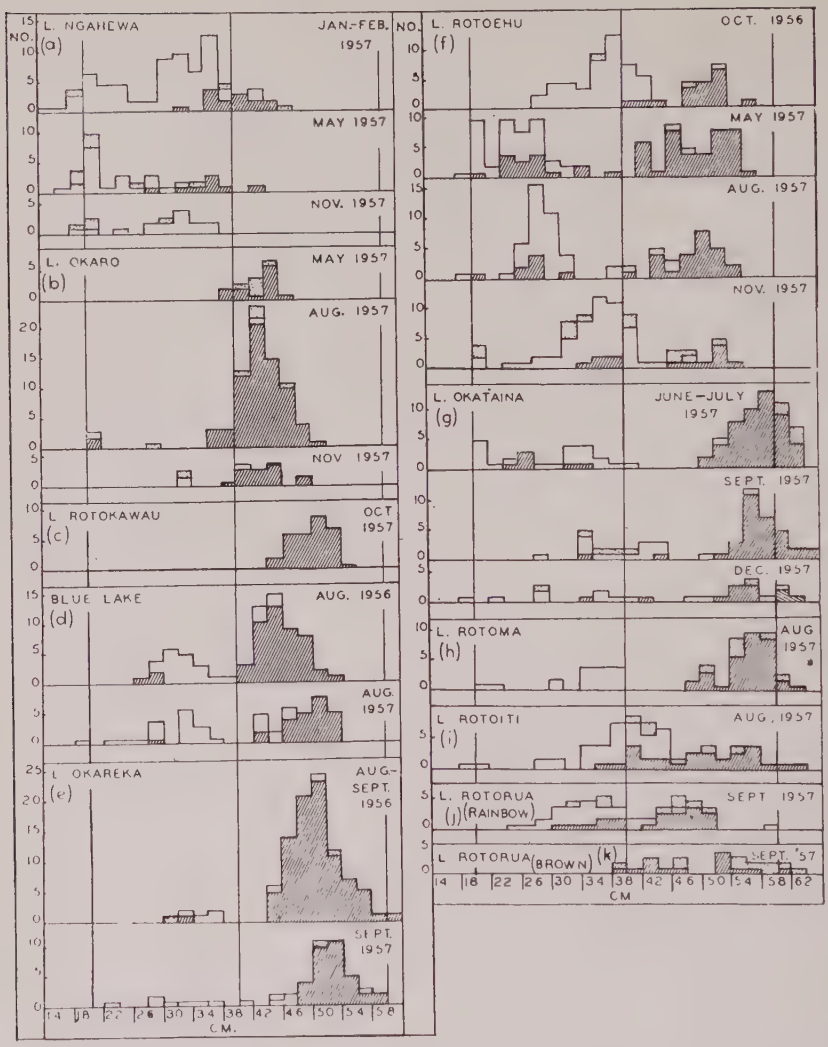


FIG. 7.—Size distributions of all major samples of fish taken in lakes other than Lake Ngapouri in 1956 and 1957. White areas represent immature fish, cross-hatched areas mature fish, and stippled areas are doubtful.

## *Lake Okaro*

Figure 8 shows the returns from tagged fish in L. Okaro between November 1956, and November 1957. Two types of fish are represented; the hatchery fish, introduced in November 1956, and the L. Okaro fish taken by gill-nets. Six of the former and four of the latter have been recaptured. As in L. Ngapouri, the immature hatchery fish

TABLE 11.—The Principal Features of the Trout Populations of the Lakes Studied, Except L. Ngapouri. In the Sex Ratio Column x and xx Denote that the Departure from Equality is Significant at the 5% and 1% Levels Respectively.

| Lake | Sample date | Modes (cm) | | | Rate of catch (all samples) | Estimated population (shore-line) | Estimated population (area) | Sex ratio (% females) | |
|---|---|---|---|---|---|---|---|---|---|
| | | Small | Medium | Large | | | | Young | Old |
| Ngahewa | Jan.-Feb. 1957 | 20-21 | — | 35-36 | 0·75 | 70 | 110 | 70xx | 68xx |
| | | *or* 20-21 | 33-34 | 40-41 | | | | | |
| | May 1957 | 20-21 | ? | ? | | | | | |
| | Nov. 1957 | 16-19 | | 30-35 | | | | | |
| Okaro | All | ? | — | 42-43 | 2·4 | 800 | 515 | ? | 36xx |
| Rotokawau | Oct. 1957 | — | — | 50-51 | 2·2 | 1100 | 520 | — | 6xx |
| Blue | Aug. 1956 | 30-31 | — | 44-45 | 0·9 | 1300 | 400 | 47 | 30xx |
| | Aug. 1957 | 32-33 | — | 50-52 | | | | | |
| Okareka | Aug.-Sept. 1956 | 32 | — | 50-51 | 2·0 | 6400 | 1550 | 69 | 36xx |
| | Sept. 1957 | 32 | — | 50-53 | | | | | |
| Rotoehu | Oct. 1956 | 38-39 | — | 50 | 3·8 | 29,000 | 13,500 | 51 | 59 |
| | May 1957 | 24-25 | — | 50 | | | | | |
| | Aug. 1957 | 28-29 | — | 50 | | | | | |
| | Nov. 1957 | 20-21 | 36-37 | 50 | | | | | |
| Okataina | June-July 1957 | 28-29 | — | 58-59 | 5·1 | 52,500 | 13,000 | 46 | 44 |
| | Sept.-Dec. 1957 | 38-39 | — | 56-57 | | | | | |
| Rotoma | Aug. 1957 | 35-36 | — | 56-57 | 1·8 | 21,000 | 3,900 | 56 | 35 |
| Rotoiti | Aug. 1957 | ? 20 | 40-41 | 54-55 | 1·3 | 44,000 | 6,400 | 49 | 26* |
| Rotorua (Rainbow) | Sept. 1957 | 34-35 | — | 46-47 | 0·9 | 65,000 | 3,000 | 43 | 60 |
| Rotorua (Brown) | Sept. 1957 | 42-43 | — | 56-57 | 1·0 | 65,000 | 3,000 | — | 43 |

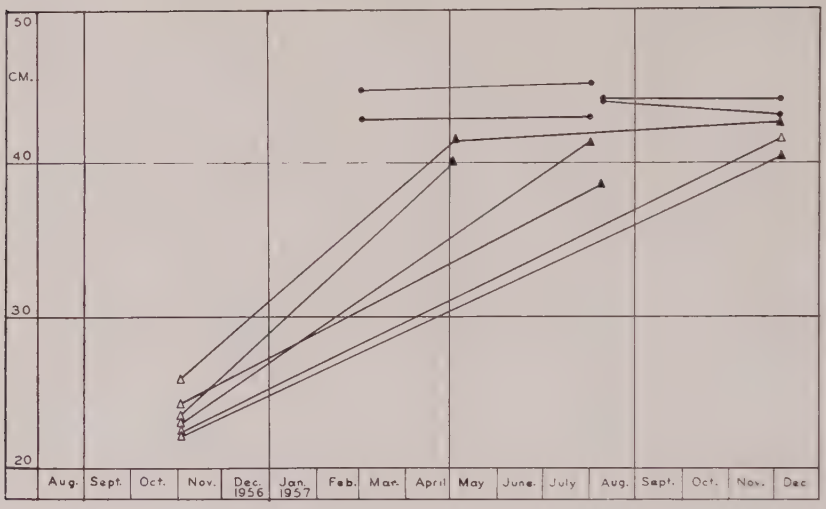


FIG. 8.—Growth of tagged fish in Lake Okaro. Symbols as in Fig. 4.

grew at about 18 cm a year or 1·5 cm a month; the mature Okaro fish failed to grow.

The older group is almost certainly a composite one; the August and November 1957 sample contained 5 fish which were tagged as yearlings in November 1956, and were hence just 2 years old when taken, and also fish which were stocked at 1 + in February 1955, and were 4 years old when taken. The few fish less than 34 cm that were taken are probably 1-year-olds.

The best estimate of the size of the population of fish in the larger size group can be obtained from the recaptures of tagged fish, assuming as before a differential mortaliy of 33% per annum among the tagged fish prior to the date of recapture. The combined estimate based on four netting operations is 340 fish with 95% confidence limits of 194 and 1407. The estimates obtained from the rate of catch by the gill-nets are well within these limits.

A similar figure would be obtained from the recaptures of the 1100 1 + fin-clipped fingerlings liberated in February 1955, if a mortality rate of between 40% and 50% per annum is assumed. In view of the almost complete absence of natural enemies of large trout other than anglers, and of the fairly sparse population, this does not seem unreasonable.

The predominance of the introduced fish as shown by the recaptures of marked fish and the scarcity of young shows that natural spawning is poor. It appears responsible for only about a quarter of the larger fish in the lake.

*Lake Rotokawau*

No fish have been liberated in L. Rotokawau for at least 6 and probably 10 years, but the fish taken did not have the characteristic appearance often found in old fish. If spawning does occur it must take place on the lake shore since there is no stream suitable for spawning.

The almost complete predominance of males is remarkable.

*Blue Lake*

The smaller group in each year is probably 1 year old, giving growth rates of about 31 cm in the first year and 15 cm in the second.

Although Blue Lake is similar to L. Rotokawau in having no spawning streams and in having had no liberations for 6 years or more, the nature of the stock is quite different. There are numerous young fish, and the stock seems to be maintaining itself.

*Lake Okareka*

If the smaller group is composed of one-year-old fish, growth is about 30 cm in the first year. Second-year growth is about 18 cm.

The proportion of young fish is low, and this probably results from the poor spawning streams. The lake was stocked with 30,000 fry in 1953 and 4600 yearlings in 1954 and these may have been largely responsible for the big peak of older fish in 1956 when they would have been three years old.

The significant excess of males among the mature fish may have been influenced by the fact that the 1956 sample was obtained in an area where spawning fish were aggregated.

*Lake Rotoehu*

Three groups of fish can be traced and provide data regarding growth. The large fish of October 1956 show no sign of further growth and ultimately become merged with younger fish. The small fish of October 1956 are possibly still identifiable as the smaller fish in the larger group in May 1957, but after this they become indistinguishable. This indicates a fairly even growth over this period at slightly over 1 cm per month, but no growth thereafter. The small fish of May 1957 can be clearly traced through the three samples taken in this year and were growing rapidly. At first sight, growth was slower between May and August but the May sample may have been truncated since the nets took few fish below 20 cm. Assuming these fish were hatched in 1956, growth in the first year is about 32 cm.

The large total population and the large population of young fish are indicative of the good spawning available, for no fry have been liberated recently.

The rather higher proportion of larger fish in 1956 may be due to the 5600 yearlings stocked in 1954, some of which would have sur-

vived to be 3-year-olds in 1956, but most of which would have probably died by 1957.

Some comparison between the fish caught by anglers and the actual population is also possible for this lake. Figure 9 compares the records supplied by the Department of Internal Affairs of anglers' catches during April 1957, and the net catches during the following May. (Note that the length groups in the graph are in inches, not centimetres.) The size limit of 14 in. clearly causes anglers at this time to take nothing but rising 2-year-old (1+) and older fish. The rising 1-year-olds (0+) are entirely spared.

*Lake Okataina*

The older fish did not show any growth in the period of the observations. The growth of the young fish is rather irregular; there was apparently rapid growth from June-July to September but none thereafter, although the December sample is rather small.

The proportion of young fish, while much lower than in L. Rotoehu, suggests a reasonable balance. Natural spawning occurs in the tributaries and in places along the lake shore while the lake was also stocked with 110,000 fry in November 1956. The proportions of young fish in September 1957, derived from these two sources, are impossible to determine.

Since many fish were taken in June-July and in September on a shallow beach where spawning fish tended to congregate, the population estimates in the table will tend to be too high.

The only significant departure from equality in the sex ratio occurred in the September sample of spawning fish when 28 mature males and only 5 mature females were taken. This may be compared with the excess of males taken in L. Okareka in 1956 under similar conditions.

*Lake Rotoma*

If the two major groups are 1-year-olds and 2-year-olds, the growth rate is about 32 cm in the first year and 20 cm in the second.

There is a moderate population of small fish, as in L. Okataina. Here, also, natural spawning is poor, only a little being possible in the tributaries; the lake was stocked with 23,000 fry in 1956.

As in L. Okataina, the population estimates will be high due to sampling on beaches where there were spawning concentrations.

*Lake Rotoiti*

The division between the groups is not as distinct as in most lakes but the two main groups probably represent, as usual, 1-year-old fish, and 2-year-olds and older fish. Growth in the first year is, then, about 40 cm and in the second 14 to 15 cm.

On this interpretation there appears to be a large proportion of young fish; spawning facilities in L. Rotoiti are limited but the fish have access to the L. Rotorua tributaries and to the Ohau Channel.

Table 12 shows an unusually high proportion of mature fish in the smaller size group. However, on account of the overlap in their size ranges the age groups are probably not separated as accurately in L. Rotoiti as in the other lakes. There is therefore no reason to assume that the incidence of maturity among the younger and older groups differs from that in the other lakes.

### *Lake Rotorua*

#### (Rainbow Trout)

The smaller fish are presumably 1-year-olds, and the larger the usual composite group. Growth is about 34 to 35 cm in the first year and 12 cm in the second. The wide spread of the smaller group in this lake and L. Rotoiti may perhaps be accounted for by the fact that some spawning occurs in the tributaries of L. Rotorua almost throughout the year, so that young fish are being added to the stock continuously. In L. Ngapouri on the other hand, spawning is limited almost entirely to July and August.

The young fish are well represented as would be expected from a lake with such good spawning streams.

As in L. Rotoiti the unusually high proportion of mature fish in the smaller size group may be due to incomplete age separation.

#### (Brown Trout)

The size distribution of the single sample of brown trout from this lake (Fig. 7 (k)) is strikingly different from that for rainbow trout. Two groups of fish can be distinguished, but the absence of any fish less than 38 cm makes interpretation almost impossible.

Since both size groups are mature it appears that in this species, unlike the rainbow trout in the same lake, growth continues after maturity. If this is so, there is a very considerable difference in the age-growth-reproduction complex between the two species.

The preliminary estimate suggests that the two species are approximately equally abundant in L. Rotorua.

## DISCUSSION

Figures 5 and 7 and Table 7 give the size of the fish in the lakes examined. The largest fish came from L. Okataina with L. Rotoma next. L. Ngahewa provided the smallest fish. It is interesting to note that no exceptionally large fish were taken in the nets and that anglers have caught larger specimens. Fish of 7 lb have been reported on occasion from L. Rotoehu and fish of 8 to 10 lb not infrequently from L. Okataina, but the heaviest fish taken in the nets from these lakes were 5½ lb and 7 lb respectively. On the other hand, as Fig. 9 shows, the average size of fish in the angling catch was slightly less than that of the net-caught fish would be if the same size limit (14 in.) was applied to them also.

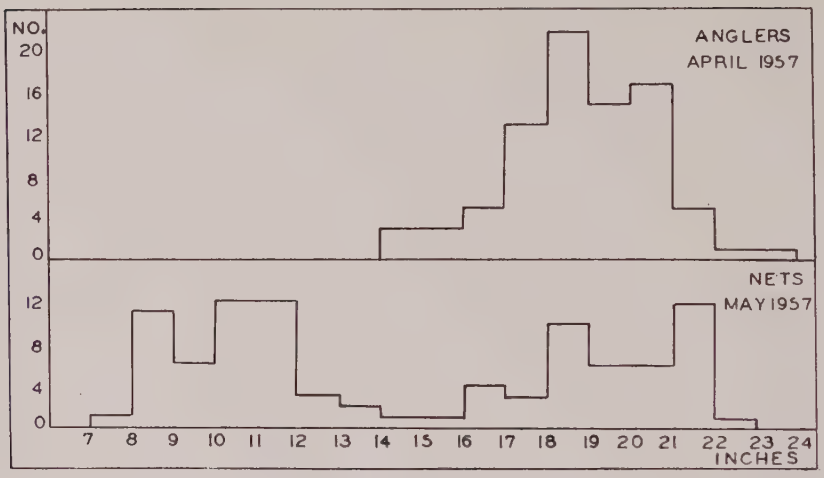


FIG. 9.—Comparison of the size distributions of fish taken in Lake Rotoehu by anglers and by nets in April and May 1957, respectively.

The estimates of population obtained above must be treated with caution but the figures may give an idea of the order of the size of the various populations. The estimates for L. Ngapouri and L. Okaro are the most accurate, being derived directly from the recapture of tagged fish. The estimates for the other lakes are derived from these by comparison of rates of catch; they are therefore subject to additional sources of error. It should be emphasised that the estimates are of older fish only and do not include fry or 1-year-olds.

Particularly in the larger lakes the differences between the estimates based on area and those based on shoreline are very considerable. The former are consistently the higher. The actual distribution of fish within a lake will depend on the shape of the basin; the deeper the lake, the more the fish are likely to be concentrated near the shore. The pairs of estimates in Table 11 are therefore likely to represent the two ends of the probable range, the position of the actual value within the range being likely to depend on the shape and depth of the lake. In shallow lakes such as L. Rotoehu and L. Rotorua the estimate based on area is probably more nearly correct, but in deep lakes like L. Okataina the length of shoreline may provide a better basis. In L. Okaro, where an independent and more reliable estimate based on the recapture of marked fish is available, the estimate based on shoreline is in better agreement.

The results show also the high proportion of brown trout in L. Rotorua, where they were approximately equal in numbers to the rainbow trout. The difference from L. Rotoiti, where only 1·5% of the catch consisted of brown trout, is particularly interesting since the two lakes are connected by a wide and relatively short channel through which fish can pass freely. None of the other lakes has any

connection by water with this system and none contain any brown trout.

The results of this survey have shown that in all the lakes the trout grow rapidly and that most of them mature at 2 years. The estimates of growth from the repeated samples and the tagged fish in L. Ngapouri are in close agreement, and again the growth estimate from the repeated samples and that from the 1957 length-frequency histograms in L. Ngapouri, L. Rotoehu, and L. Okataina agree well enough to confirm the use of these histograms for general growth estimates; some year to year variation occurred but was not serious.

There is some evidence that in both 0 + and 1 + groups, growth slowed down in the winter and again in the summer. Results obtained from L. Ngapouri in February 1958 show this clearly. While the median of the 1957 young group rose steadily from 25 cm to 31 cm in 15 weeks between July and October, it only rose another 1·5 cm in a similar period from October to February. Two L. Ngapouri fish tagged in December and recaptured in February grew 1·1 cm and 1·4 cm in 10 weeks and 9 weeks respectively, growth which agrees closely with the group figures.

In contrast, mature fish make little or no further growth. This is evident from the L. Ngapouri tagging results and is directly supported by the repeated samples from L. Rotoehu and L. Okataina. It appears, however, that immature fish of the same age may continue to grow and hence this abrupt cessation of growth is closely associated with maturity. The completeness of the cessation may, however, depend on the balance between the fish population and the food supply, since in other lakes rainbow trout continue to make some growth after reaching maturity.

This change in growth in the mature fish means, as has already been pointed out, that the older group is composed of fish of two or more ages. There appears to be a tendency for the immature fish in the older group to fall below the average size; these fish would probably be mainly 2-year-olds and, unless they are growing more slowly than the mature fish, this would suggest that there is a definite although small difference in size between the two age groups. The error caused by taking the median of the larger group as representing the median of the 2-year-old fish will, however, probably be small, although the second-year growth may tend to be over-estimated.

The apparent decrease in size of the larger fish which occurs in L. Okataina (Fig. 7 (g)) may be due to the death of older and slightly larger fish after spawning, leaving the younger and smaller fish.

There is little data available as to the age composition of the fish in the large group in which growth has stopped. In Lake Okaro 75% of the stock is composed of 4-year-old fish derived from the liberation in 1953. The occurrence of immature fish among the group of larger fish may also give a clue to the general age structure of the group, for the older the fish the more likely they are to have matured. L. Okaro shows only 2 immature fish, L. Okareka 3 (2 in 1956 and 1 in 1957), L. Rotokawau none at all. Blue Lake, however, has a moderate pro-

portion of immature fish in this group, which again suggests that this is a younger stock than the other lakes where recruitment is poor.

The occurrence of mature fish in the group of smaller fish shows some interesting features. The lakes can be divided into three groups in this respect. In L. Rotorua and L. Rotoiti about one-quarter of the fish in this group were mature; in L. Rotoehu and L. Okataina about one-third of the males but very few of the females were mature; in the remaining lakes very few fish of either sex were mature. It has already been suggested that the high proportion of mature fish in the small group in the first two lakes may be due to incomplete age separation resulting from a prolonged spawning season, but the cause of the differences between the other two groups of lakes is still obscure. The mature fish fall about the average size of their age group and they may be either 1-year-old fish maturing early or stunted 2-year-olds.

Finally, the sex ratios demand some discussion. Tables 10, 11, and 12 show that the young fish generally show little variation from the 50:50 ratio. The difference is only significant in L. Ngapouri and L. Ngahewa and in both it is the females that predominate. L. Okareka also shows a high percentage of young females but the number of fish is small and the difference from equality is not significant.

The older fish show a completely different picture. The females predominate significantly in only one lake (L. Ngahewa); they also outnumber the males in L. Rotoehu but not significantly. The males, however, predominate significantly in L. Okaro, L. Rotokawau, Blue Lake, L. Okareka, and L. Rotoiti; they are also more numerous in L. Okataina and L. Rotoma but not significantly. The sexes were evenly balanced in L. Ngapouri and L. Rotorua.

L. Okaro, L. Rotokawau, and Blue Lake have no spawning streams flowing into them, while L. Okareka, L. Okataina, and L. Rotoma have only limited spawning facilities. By contrast L. Rotoehu, L. Ngapouri, and L. Ngahewa have good spawning streams. It has also been suggested that owing to these poor spawning facilities and little or no stocking, L. Okaro, L. Rotokawau, and to a lesser extent L. Okareka, have ageing stocks. There seems, therefore, to be an association between lack of spawning streams, ageing stocks, and a preponderance of males. The almost equal sex ratios of the young in nearly all the lakes show that the difference in the adults is due to a differential mortality. The inability of many of the females to shed their eggs may perhaps cause an increased mortality among them. Alternatively, failure to spawn may reduce the mortality rate of the males. The excess of females in L. Ngahewa which occurs also among the immature fish is very striking. This lake has a good spawning stream. The unusual sex ratio may be associated with low growth rate which is found in this lake.

## Feeding Habits

### *Material and Methods*

Data were obtained from all the lakes investigated, and the samples used for this purpose were all taken by gill-nets. Only the contents of

the stomachs and oesophagi of the fish were recorded. Usually the main categories of organisms were reasonably easy to identify, but occasionally, especially in hot weather and when the fish were not examined for some time after death, the contents could not be identified or could only be generally identified (e.g. classed only as "fish" or "insects").

CATEGORIES

*Empty*—This includes fish with nothing in the stomach and also fish with stones, sticks, or weed only. The percentage is expressed as that of the total number of fish in the sample. The percentages of fish with different food organisms in the stomach, however, are expressed as those of the number of fish with some food, fish with empty stomachs being excluded from the total.

*Smelt*—(*Retropinna* sp.)

*Other fish*—This includes all fish, other than smelt, and also unidentified fish. The most frequent of these was the bully (*Gobiomorphus* sp.). This other fish found in the stomach contents were: (i) galaxiids (probably *G. koaro*) which formed all but one of the "other fish" of L. Rotoiti but which occurred nowhere else except once in L. Okataina; (ii) trout, which occurred once each in L. Okataina, in L. Rotoehu, and in L. Okaro, and trout eggs, which were found in stomachs of several trout in L. Rotoma and in one fish each in L. Okataina, in L. Okareka, and in L. Rotorua; and (iii) gold fish (*Carassius auratus*), which were found in three fish in L. Rotoehu.

*Molluscs*—Principally *Isodora* and *Potamopyrgus*;

*Paranephrops*—Freshwater crayfish (koura);

*Insects (aquatic)*—Includes larvae and imagines of primarily aquatic insects (e.g. chironomids and Odonata). Imagines, however, were very uncommon.

*Insects (Terrestrial)*—Includes wholly terrestrial insects (e.g. Hymenoptera and some Coloeptera).

*Insects (all)*—The total is not necessarily the sum of the aquatic and terrestrial since a fish with both in its stomach is only listed once; such fish were surprisingly rare. Unidentified insects are also included in the total even if they cannot be ascribed to the subclasses.

*Others*—Includes tadpoles, frogs, and any unidentified animals.

*Smelt only, etc.*—These fish have been feeding exclusively on one category of organisms.

TABULATION—The results are summarized in Table 13. The figures are of the number of occurrences of fish with particular foods in their stomachs, i.e. fish containing smelt and insects are listed under both. No estimation was made of the amount of food in the stomach; as a

TABLE 12.—The Distribution of the Sexes, and of Maturity, in the Samples Taken from the Principal Lakes. The Samples have been Subdivided into Large and Small Size Groups According to the Size Distributions Shown in Fig. 5. In Lake Ngahewa and Rotoehu it was Necessary to Apply Different Size Limits to Samples Taken at Different Times in Order to Separate the Groups Satisfactorily.

| Lake | Size (cm) | Mature ♂ | Mature ♀ | Immature ♂ | Immature ♀ | Unclassified | % Mature ♂ | % Mature ♀ | Total |
|---|---|---|---|---|---|---|---|---|---|
| Ngahewa | > 28-32 | 6 | 15 | 16 | 33 | 2 | 27 | 31 | 30 |
| | < 28-32 | 1 | 0 | 14 | 37 | 11 | 7 | 0 | 2 |
| | Total | 7 | 15 | 30 | 70 | 13 | 19 | 18 | 18 |
| | % | 32 | 68 | 30 | 70 | — | — | — | — |
| Okaro | > 35 | 64 | 36 | 1 | 2 | 6 | 98 | 95 | 97 |
| | < 35 | 2 | 0 | 1 | 2 | 2 | 67 | 0 | 40 |
| | Total | 66 | 36 | 2 | 4 | 8 | 97 | 90 | 95 |
| | % | 65 | 35 | 33 | 66 | — | — | — | — |
| Rotokawau | Total | 29 | 2 | 0 | 0 | 0 | 100 | 100 | 100 |
| | % | 94 | 6 | — | — | — | — | — | — |
| Blue | > 38 | 49 | 21 | 9 | 4 | 0 | 84 | 84 | 84 |
| | < 38 | 4 | 0 | 16 | 18 | 0 | 20 | 0 | 11 |
| | Total | 53 | 21 | 25 | 22 | 0 | 68 | 49 | 61 |
| | % | 72 | 28 | 53 | 47 | — | — | — | — |
| Okareka | > 48 | 80 | 46 | 2 | 1 | 3 | 98 | 98 | 98 |
| | < 48 | 0 | 1 | 4 | 8 | 0 | 0 | 11 | 8 |
| | Total | 80 | 47 | 6 | 9 | 3 | 93 | 85 | 89 |
| | % | 63 | 37 | 40 | 60 | — | — | — | — |
| Rotoehu | > 40-46 | 35 | 50 | 4 | 5 | 4 | 90 | 91 | 90 |
| | < 40-46 | 30 | 2 | 64 | 95 | 9 | 32 | 2 | 17 |
| | Total | 65 | 52 | 68 | 100 | 13 | 49 | 34 | 41 |
| | % | 56 | 44 | 40 | 60 | — | — | — | — |
| Okataina | > 46 | 50 | 42 | 4 | 1 | 6 | 93 | 98 | 95 |
| | < 46 | 10 | 0 | 19 | 24 | 5 | 34 | 0 | 19 |
| | Total | 60 | 42 | 23 | 25 | 11 | 72 | 63 | 68 |
| | % | 59 | 41 | 48 | 52 | — | — | — | — |
| Rotoma | > 42 | 24 | 13 | 0 | 0 | 4 | 100 | 100 | 0 |
| | < 42 | 0 | 0 | 7 | 9 | 0 | 0 | 0 | 0 |
| | Total | 24 | 13 | 7 | 9 | 4 | 77 | 59 | 70 |
| Rotoiti | % | 65 | 35 | 44 | 56 | — | — | — | — |
| | > 48 | 13 | 5 | 1 | 0 | 1 | 93 | 100 | 95 |
| | < 48 | 7 | 6 | 16 | 16 | 4 | 30 | 27 | 29 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Total | 20 | 11 | 17 | 16 | 5 | 54 | 41 | 48 |
| | % | 65 | 35 | 51 | 49 | — | — | — | — |
| Rotorua | > 43 | 6 | 8 | 0 | 1 | 6 | 100 | 89 | 93 |
| (Rainbow) | < 43 | 4 | 3 | 12 | 9 | 3 | 25 | 25 | 25 |
| | Total | 10 | 11 | 12 | 10 | 9 | 45 | 52 | 49 |
| | % | 48 | 52 | 55 | 45 | — | — | — | — |
| | > 50 | 5 | 2 | 0 | 0 | 7 | 100 | 100 | 100 |
| Rotorua | < 50 | 3 | 4 | 0 | 0 | 3 | 100 | 100 | 100 |
| (Brown) | Total | 8 | 6 | 0 | 0 | 10 | 100 | 100 | 100 |
| | % | 57 | 43 | — | — | — | — | — | — |

TABLE 13.—The Frequency of Occurrence of the Main Food Animals in the Stomach Contents of the Fish Examined from Each Lake. The First Figure in Each Case Shows the Actual Number of Fish Containing that Animal; in the Second Figure this is Expressed as a Percentage of the Fish Containing some Food.

| Lake | Nga-pouri | Ngahewa | Okaro | Rotoehu | Okataina | Roto-kawau | Blue | Okareka | Rotoma | Rotoiti | Rotorua (rainbow) | Rotorua (brown) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| No. of fish | 257 | 97 | 59 | 304 | 133 | 18 | 53 | 31 | 42 | 63 | 42 | 14 |
| Empty | 45 18 | 20 21 | 7 12 | 88 24 | 36 27 | 2 11 | 8 15 | 8 26 | 15 36 | 21 33 | 7 17 | 2 14 |
| Smelt | 133 63 | 6 8 | 7 13 | 169 78 | 50 52 | 8 50 | 28 62 | 10 44 | 14 52 | 23 58 | 15 43 | 7 58 |
| Other fish | 2 1 | 32 42 | 20 39 | 11 5 | 13 13 | 2 12 | 3 7 | 2 9 | 8 30 | 5 12 | 10 24 | 8 67 |
| Molluscs | 20 9 | 4 5 | 2 4 | 14 6 | 15 15 | 0 0 | 1 2 | 5 21 | 4 15 | 9 21 | 15 43 | 1 8 |
| *Paranephrops* | 17 8 | 2 3 | 3 6 | 1 0·5 | 8 8 | 4 25 | 2 4 | 2 9 | 1 4 | 4 10 | 4 11 | 0 0 |
| Insects (aquatic) | 32 5 | 7 9 | 22 42 | 23 11 | 28 29 | 8 50 | 7 16 | 3 13 | 3 11 | 1 2 | 0 0 | 0 0 |
| Insects (terr.) | 37 17 | 22 29 | 14 27 | 33 15 | 15 15 | 9 56 | 18 40 | 10 44 | 7 26 | 8 19 | 6 17 | 0 0 |
| Insects (all) | 67 32 | 25 32 | 33 63 | 55 25 | 41 42 | 12 67 | 23 51 | 11 48 | 10 37 | 9 21 | 6 17 | 0 0 |
| Tadpoles | 5 2 | 1 1 | 0 0 | 3 1 | 2 2 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 | 0 0 |
| Unidentified | 17 8 | 21 27 | 1 2 | 7 3 | 0 0 | 1 6 | 5 11 | 2 9 | 0 0 | 5 12 | 1 3 | 0 0 |
| Smelt only | 94 44 | 5 6 | 4 8 | 127 59 | 32 33 | — — | — — | — — | — — | — — | — — | — — |
| Insects only | 23 11 | 15 19 | 20 39 | 24 11 | 21 22 | — — | — — | — — | — — | — — | — — | — — |
| Molluscs only | 5 2 | 0 0 | 0 0 | 6 3 | 6 6 | — — | — — | — — | — — | — — | — — | — — |
| Crustacea only | 10 5 | 1 1 | 0 0 | 0 0 | 5 5 | — — | — — | — — | — — | — — | — — | — — |
| Bully only | 0 0 | 0 0 | 7 13 | 0 0 | 0 0 | — — | — — | — — | — — | — — | — — | — — |

general rule only smelt (through the year) and manuka beetles (*Pyronota* sp.) (in spring) were found in dense quantities in the stomach. The results expressed in this way probably tend to indicate the relative quantities eaten. The percentages should be taken as a general indication only; among other things, the chance of any organism being recorded in the stomach contents will depend not only on how ofte it is eaten but also on how long its characteristic parts remain undigested. On the whole, *Paranephrops*, molluscs, and terrestrial insects would appear to persist longer than fish or aquatic insects; the two main kinds of fish, smelt and bully (*Gobiomorphus* sp.), can often be separated by the colour of the flesh even when well digested.

Repeated samples were taken from Lakes Ngapouri, Ngahewa, Okaro, Rotoehu, and Okataina. In the lakes netted once, or annually, the samples were taken between July and October, i.e. during the winter months. They should thus be comparable with each other and also with samples taken within this period from the other five lakes. They will not be representative of the stomach contents throughout the year, but the five repeated samples will indicate how typical they are.

## Results

### *Lake Rotoehu*

The samples from this lake are the only ones large enough and regular enough to allow of a simultaneous analysis for time and fish size, and they have been analysed in this way in Table 14. From this table it is clear that, taking all sizes of trout together, smelt predominated in the food throughout the year, although they tended to form a diminishing proportion during the period of the observations, and were at a minimum in November 1957. The proportion of insects tends to increase. Unlike previous samples, the insects in November 1957, were mainly aquatic and consisted almost exclusively of Odonata larvae and included both *Somatochlora* sp. and *Xanthagrion* sp. in roughly equal numbers. The terrestrial insects were nearly all manuka beetles (*Pyronota* sp.). The earlier samples of terrestrial insects had comprised mainly Diptera, Hymenoptera, and Lepidoptera, and aquatic insects had included a dysticid, an ephemerid and a perlid.

Examination of the variations in food with size of trout shows for a whole year a tendency for the larger fish to have a greater proportion with empty stomachs but there is wide variation from sample to sample. There is some indication that in the winter (May especially) the larger fish (40 cm and over) feed to a greater extent on insects and molluscs and less on smelt than do the smaller fish. At this time also a considerably higher percentage of fish with empty stomachs occurred among the large fish than among the small fish. Opposite tendencies appear in the summer but the samples are too small to have much significance. These points must be considered in interpreting the single samples taken from other lakes in the winter.

Molluscs, and "other fish"—here predominantly bullies—occurred rather irregularly but they were eaten more freely by the larger fish than by the smaller.

### *Lake Ngapouri*

L. Ngapouri gives the most detailed picture of temporal variations of any lake, with samples taken at about 5-week intervals over 14 months and a few smaller samples outside this period. The occurrence of the two principal foods is summarized in Fig. 10 in which the results for 1956 and 1957 are combined into a single composite year. Smelt generally predominated except in November and December; they are the only fish other than trout so far found in L. Ngapouri. In November and December the dominant food was insects, almost entirely manuka beetles. Both molluscs (mainly *Isodora* and sometimes *Potamopyrgus*) and koura (*Paranephrops*) occurred regularly in small numbers. The bulk of the aquatic insects were Odonata but a few corixids and chironomids occurred. The number of fish with empty stomachs was fairly constant.

The smaller fish showed a tendency to feed on smelt and insects whereas the larger fish also took molluscs and koura; the differences, however, are not great. It is interesting to note that koura only occurred in fish over 35 cm. There is little variation between the size groups in the percentage of fish with empty stomachs.

### *Lake Ngahewa*

The samples from this lake were irregular and only two were of any size. In addition to trout, the lake contains abundant bullies and only a few smelt. The shortage of smelt is well reflected in

TABLE 14.—The Percentage Occurrence of the Main Food Animals in the Stomachs of Trout from L. Rotoehu Analysed According to Date of Capture and Size of Fish.

| Month | October 1956 | | | November 1956-March 1957 | | | May 1957 | | | August 1957 | | | November 1957 | | | Total | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Size-Group (cm) | < 35 | 35-50 | > 50 | < 35 | 35-50 | > 50 | < 35 | 35-50 | > 50 | < 35 | 35-50 | > 50 | < 35 | 35-50 | > 80 | < 35 | 35-50 | > 50 |
| Total fish | 13 | 36 | 11 | 4 | 7 | 9 | 48 | 22 | 21 | 39 | 16 | 15 | 21 | 35 | 6 | 125 | 116 | 62 |
| % empty | 31 | 8 | 0 | 25 | 14 | 0 | 17 | 45 | 67 | 26 | 19 | 67 | 38 | 40 | 0 | 23 | 27 | 39 |
| No. full | 9 | 33 | 11 | 3 | 6 | 9 | 40 | 12 | 7 | 28 | 13 | 5 | 13 | 21 | 6 | 96 | 85 | 38 |
| % smelt | 100 | 91 | 100 | 100 | 67 | 67 | 85 | 67 | 29 | 93 | 69 | 40 | 31 | 76 | 67 | 74 | 79 | 66 |
| % other fish | 0 | 3 | 0 | 0 | 0 | 22 | 0 | 0 | 14 | 0 | 0 | 0 | 8 | 10 | 67 | 1 | 4 | 18 |
| % molluscs | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 25 | 43 | 0 | 15 | 0 | 15 | 0 | 16 | 5 | 6 | 11 |
| % total insects | 11 | 3 | 9 | 67 | 0 | 11 | 18 | 33 | 29 | 25 | 31 | 60 | 70 | 52 | 50 | 23 | 24 | 26 |
| % Others | 0 | 6 | 0 | 33 | 33 | 22 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 1 | 6 | 5 |

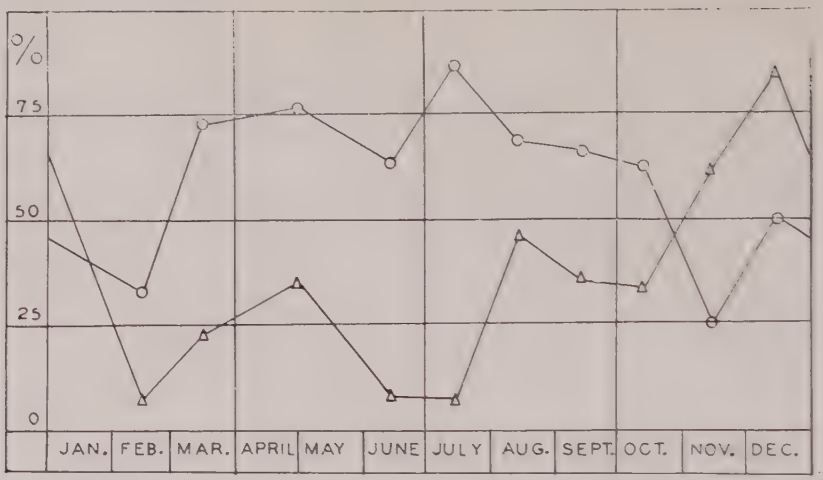


FIG. 10.—Percentages of fish of all sizes taken in Lake Ngapouri which contained smelt (circles) and terrestrial insects (triangles). Results for 1956 and 1957 combined.

the stomach contents. The full data show that bullies tended to predominate in the larger fish and insects in the small fish. Aquatic insects were mainly Odonata with occasional chironomids and culicids; the terrestrial insects were mainly Coleoptera.

Koura were found less frequently than might be expected for a lake with a large koura population. Possibly the small average size of the trout puts the koura out of their range. Terrestrial insects occur more often than aquatic.

### *Lake Okaro*

Four samples were taken but only that of August had an adequate number of fish. There appears to be little significant difference between the stomach contents at different times of the year. Both bullies and smelt occur in the lake, but while bullies are very common smelt are present only in small numbers. This is reflected in their proportions in the food. Although fish were important, insects were actually the dominant food over the data as a whole. There was a high proportion of aquatic insects, largely culicids and chironomid larvae with some Odonata; one corixid and a coleopteran also occurred.

The limited results suggest that as in other lakes the proportion of bullies increases in the larger group and that of insects decreases. The proportion of koura and mollsucs in the food was low although L. Okaro, like L. Ngahewa, has a considerable koura population.

### *Lake Okataina*

Smelt formed the main single food, although there were several trout containing bullies, four with trout eggs, and one with a fish which

was probably, but not certainly, a galaxiid. The proportion with insects was fairly high; terrestrial insects included Lepidoptera, Orthoptera (Saltatoria) and Coleoptera; aquatic insects were principally Odonata with a few corixids and one dytiscid.

Molluscs formed a regular and important proportion of the food, while koura were few and occurred mainly in the June and July samples.

The variation in feeding with size followed the familiar pattern; smelt tended to fall in importance with increasing size of trout while other fish and insects rose. Molluscs showed no definite distribution but koura occurred only in the larger fish.

*Lake Rotokawau*

From this and subsequent lakes, only single samples were taken. The sample from L. Rotokawau was small, and it was taken over two nights in October. The data show no significant effect of size except that "other fish" (bully in this case) occurred in the larger fish and that terrestrial insects (Lepidoptera, Coleoptera, and Diptera) predominated in the larger fish and aquatic insects in the smaller fish. Insects, in fact, formed the dominant food with smelt next.

*Blue Lake*

The sample was taken at the end of August. Smelt predominated in the food but insects were also numerous in the larger fish. Terrestrial insects were mainly Coleoptera, with some Lepidoptera and Diptera and one arachnid. Aquatic insects included Odonata, dytiscids, and Diptera (Culicidae).

*Lake Okareka*

This sample was taken in September. Fish and insects formed the bulk of the food; smelt again occurred principally in the smaller fish and insects, molluscs and koura in the larger. As in Blue Lake terrestrial insects were more common than aquatic; the former included Coleoptera with a few Diptera and Lepidoptera; the latter consisted only of a few corixids.

*Lake Rotoma*

This sample was taken in August. Smelt again predominated although they decreased in the larger fish. Insects occurred in over one-third of the trout but showed no correlation with size; they were mainly terrestrial insects (Diptera, Coleoptera, and Lepidoptera) but also included one Odonata and a Corixid. The "other fish" were entirely trout eggs.

*Lake Rotoiti*

This sample was taken in July and August. Smelt again predominated, and decreased in importance in the larger fish. Galaxiids also occurred

and this was the only lake, except possibly L. Okataina, where these fish appeared in the food. Molluscs and koura occurred only in the larger fish: insects occurred in all sizes and were again mainly terrestrial (Lepidoptera, Coleoptera, and Hymenoptera). A rather larger percentage of trout had empty stomachs.

*Lake Rotorua (Rainbow Trout)*

This sample was taken in September. Fish formed the bulk of the food, with smelt predominating in the smaller fish and bully in the larger. Molluscs were common in all groups; koura occurred in the larger fish only and insects (all terrestrial) in the smaller only.

*Lake Rotorua (Brown Trout)*

This sample was taken concurrently with the rainbow trout from this lake. All but one of the trout had fish in the stomach; although in the total bullies and not smelt predominated, there was the usual pattern of mainly smelt in the smaller fish and bully in the larger. Numbers, however, were rather small.

## DISCUSSION

The L. Rotoehu samples have shown that there may be considerable changes in the proportion of organisms in fish of different sizes at different times of the year. In particular, smelt may form a smaller proportion and insects a larger proportion of the food of the bigger fish during the winter than during the rest of the year. Since the eight single samples were all taken during the winter, this bias must be borne in mind when interpreting the results. However, as the totals from the repeated samples show, this seasonal effect does not account for the difference found between fish of different sizes in the eight single samples.

It should be noted that due to the method of analysis, percentages of different foods are independant and a high percentage of one organism does not ipso facto affect the percentage of the others.

The results from all the lakes show that the trout generally feed mainly on smelt, and other organisms predominate only when smelt are not available. They may be unavailable either because they are few (i.e. L. Ngahewa, L. Okaro) or because they move offshore in warm weather, as Dr V. H. Jolly has found in the large lakes (pers. comm.): this may have happened in November 1957, in L. Rotoehu, when the proportion of smelt in the food of trout taken round the shore was low. In certain cases, however, trout may show a preference for other food although smelt are available; for instance, many of the larger fish feed on bully or galaxiids, and in L. Ngapouri and other lakes in November and December, the trout took large numbers of manuka beetles.

It is interesting to note that smelt tended to occur particularly in the smaller fish and that they were found in the smallest fish so far taken

from the lakes (12 cm) and also in fry in the L. Ngapouri tributary stream. This is opposite to the feeding pattern described for brown trout in the Horokiwi stream (Allen, 1951), where the fish apparently fed on animals approximately proportion to their size and only the large trout ate fish. The lakes, however, differ from the streams in the apparent absence of small insects, and the preponderance of terrestrial insects rather than aquatic in the food of most stocks is significant. Further, the L. Ngapouri tributary from which the fry were taken is extremely unstable and does not support a rich bottom fauna. Smelt, especially young smelt, may thus form the most readily eaten food for young trout. The sizes of the fish in the trout stomachs were not recorded, but the smelt were probably generally 3 to 5 cm in length; the bullies would be of about the same length or slightly longer but have considerably stouter bodies. The fact that the proportion of trout which were eating bullies is almost invariably proportional to the size of the trout, and is only high in smaller fish when smelt are not available, may actually be in accordance with the principles found in the Horokiwi, since the bully is a more bulky fish than the smelt and may grow to a greater size. The proportion of fish eating koura also tended to increase with increasing size of trout.

The rarity of trout in the stomach contents is notable: only three fish out of 1113 examined (0·27%) had trout fry or fingerlings (one in each fish), and only 13 (1·17%) had trout eggs in the stomach. These figures may, however, not represent truly the extent to which they are eaten when available; the eggs for instance will usually only be available for two months or so. Thus, in L. Rotoma in August six of the 42 feeding fish examined had eggs in the stomach. Fry and fingerlings, however, will be available in a good deal longer—from four to six months or more depending on the lake—and so the amount eaten even when they are most readily available will probably not exceed 1% of the total amount of food eaten.

It is interesting to note the number of trout with trout eggs in the stomach in L. Rotoma. This is a lake with poor spawning streams and many fish spawn in the sand and gravel of the lake edge. The eggs are thus more exposed to the feeding fish than they would normally be. Three fish in L. Okataina and one in L. Okareka (both lakes with poor spawning streams) had trout eggs in the stomach.

Koura form a smaller percentage of the food than might be expected, especially in lakes like L. Ngahewa and L. Okataina. It is interesting that although even young koura should persist in the stomach at least as long as smelt, no small koura (less than 5 cm) were ever seen in the stomach contents. In L. Okataina koura were observed by diving to be abundant down to at least 70 ft in January 1958 (R. M. Cassie, pers. comm.).

Of the insects in the food, the proportion of terrestrial forms is relatively large and only in L. Okaro and L. Okataina did aquatic insects predominate. This is probably due to the rather sparse bottom fauna, particularly of insects, and perhaps to a greater tendency for flying terrestrial insects to land on the open expanse of a lake than

on the relatively narrow water-way of a stream. Of the aquatic insects which included all such forms whether taken on the surface or on the bottom, by far the biggest proportion were Odonata nymphs, and generally *Somatochlora*, although *Xanthagrion* was common in L. Rotoehu. Chironomids occurred rather rarely; their larvae, however, together with small annelids form the great bulk of the bottom fauna of the open water in lakes such as L. Okaro.

Molluscs occurred frequently only in L. Rotorua; they occurred in about one-fifth of the fish from L. Rotoiti, L. Rotoma, L. Okareka, and L. Okataina.

Tadpoles appeared in the food of fish from many lakes but in insignificant numbers.

## REFERENCES

ALLEN, K. R., 1951: The Horokiwi Stream: A Study of a Trout Population. *Fish. Bull. Wellington, N.Z.* : 10.

ALLEN, K. R.; CUNNINGHAM, B. T., 1957: New Zealand Angling, 1947-1952: Results of the Diary Scheme. *Fish. Bull. Wellington, N.Z.* : 12.

DELURY, D. B., 1958: The Estimation of Population Size by a Marking and Recapture Procedure. *J. Fish. Res. Bd. Can., 15*. 27-45.

GRANGE, L. I., 1937: The Geology of the Rotorua-Taupo Subdivision, Rotorua and Kaimanawa Divisions. *N.Z. geol. Surv. Bull.* (n.s.), 37.

# INTENSITY VARIATIONS OF THE COSMIC RAY NUCLEONIC COMPONENT

By M. A. Collins*, Physics Department, Victoria University of Wellington

*(Received for publication, 16 April 1959)*

***Summary***

Measurements are presented of the nucleonic component of cosmic rays observed at Wellington, New Zealand. A 27-day recurrence is demonstrated but the increased counts show no tendency to be confined to the impact zone times of 04, 09, and 20 hours calculated by R. Lust. Consequently it seems unlikely that the increases are due to particles coming directly from the sun. The suggestion of E. N. Parker that ionic clouds from the sun deflect particle streams originating elsewhere seems preferable.

## Introduction

The cosmic ray nucleonic component can be defined as that part of the total secondary radiation which produces low energy neutrons in interactions with matter. Study of neutron production in the atmosphere has shown that moderate energy nucleons (protons and neutrons) are the major slow neutron producers (Cocconi *et al.*, 1950) and a small contribution is made through interactions of $\pi$ mesons (Simpson *et al.*, 1953).

Cosmic ray primary particles interact with air nuclei to produce a variety of secondary particles in which are included nucleons and mesons. Treiman (1952) has shown that primary particles of lower energy spend most of their energy in nucleon production whereas those of higher energy spend their energy chiefly in meson production. This deduction is supported by the experimental observation of a large latitude dependence of the nucleonic component intensity (Simpson *et al.*, 1953). Hence the nucleonic component provides a convenient means of study of the low energy component of the primary radiation.

The expectation that the influence of solar activity on cosmic rays would be observed in the low energy portion of the primary spectrum has made the study of the nucleonic component important in determining the extent of solar influence on cosmic radiation. The Chicago group, headed by Simpson, has developed the Neutron Monitor Pile (Simpson, *et al.*, 1953) for the continuous recording of nucleonic component intensity. With this instrument, cosmic ray intensity variations of 27-day and 11-year periods, which correspond to activity cycles of the sun, have been observed.

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A question raised in the study of solar influence on cosmic rays is whether or not the sun emits cosmic ray particles. This question has received a great deal of attention in the literature (Meyer *et al.*, 1956). Firor (1954) has calculated Stormer orbits for particles approaching the earth from the direction of the sun. He has found the zones to which particles of a given energy are focussed by the earth's magnetic field. These zones—so called impact zones—he found at 0400, 0900, and 2000 hours geomagnetic local time. Analysis of the large cosmic ray increases indicated that the effect was consistent with particles approaching the earth from the direction of the sun. Jory (1956) and Lust (1957) have extended the impact zone theory and have had some success in explaining cosmic ray phenomena during solar flares.

## Apparatus

Neutron monitor piles were used as detectors. The piles consist of boron tri-fluoride proportional counter tubes surrounded with paraffin, thus forming a slow neutron detector. A 2 in. thickness of lead is used to induce neutron production in the vicinity of the counting element. A cross-section of the two piles (referred to as A and B) is shown in Fig. 1. The outer paraffin shown in this figure acts as a shield against slow neutrons produced in the equipment about the piles.

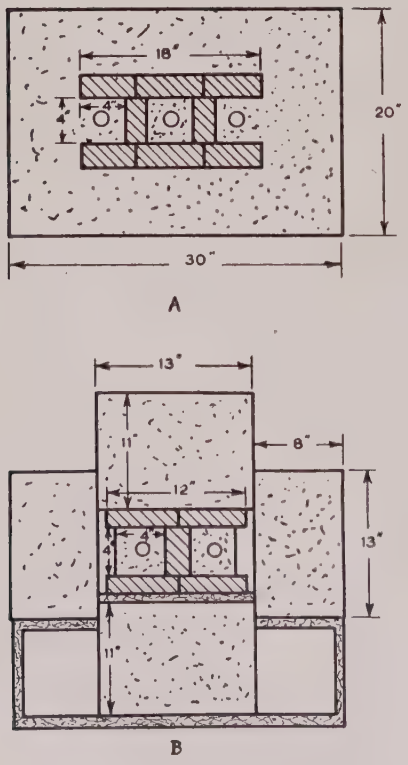



FIG. 1.—Cross-sectional view of neutron monitors used.

The counting circuits of both piles were similar. The head amplifiers in each case were situated as close as possible to the counter tubes. The main amplifiers were followed by Schmidt discriminators to distinguish neutron counts from background noise and gamma quanta, etc. These units were similar to those suggested by Elliot (Simpson, 1955).

The pulses were scaled on Philips E.1.T. decade sealing valves. Pile A was scaled by a factor of 10 and Pile B (which had a higher counting rate as it employed counter tubes filled with $BF_3$ gas enriched to 98% of the $B^{10}$ isotope) was scaled by a factor of 100. The scaled counts were recorded on a paper tape.

## RESULTS

Simpson *et al.* (1953) have shown that the nucleonic component possesses a negligible temperature coefficient. Thus, meteorological corrections are limited to a correction for atmospheric pressure changes. Since cosmic ray intensity is exponentially dependent on pressure, a logarithmic correction of the form

$$R_c = R_o \, e^{-\alpha \Delta \rho}$$

where $R_c$ = corrected counting rate,
$R_o$ = observed counting rate,
$\Delta\rho$ = deviation of pressure from a standard value,
and $\alpha$ is the pressure coefficient,

has been used in correcting all data (Wada, 1957).

The pressure coefficient, $\alpha$, determined by Sudman (1954) was used, as disturbed conditions during the presently described observation did not allow such a determination. Atmospheric pressures were obtained from the New Zealand Meteorological Office in Wellington, which is at essentially the same altitude as the monitors, and nearby.

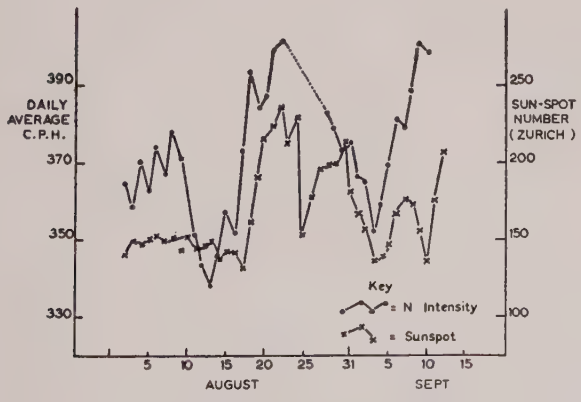



FIG. 2.—Count-rate and Sunspot Numbers (Zürich) for August-September period 1956.

The number of counts for every half-hour period was obtained from the recorder, and these were pressure corrected and tabulated. The statistical and scaling uncertainties were tabulated for each period.

Figure 2 is a plot of daily average counting rates (in counts per hour) for a typical section of the observed period. The lower curve is the sunspot number, as observed at Zürich, and, in general, the experimental results shown suggest a positive correlation, rather than

the generally accepted negative correlation, over the short time interval shown. Further work on this observed correlation will be carried out.

Two periods, 14 December 1956 to 6 March 1957, and 10 May 1957 to 28 July 1957 were chosen at random and investigated for the existence of 27-day variations.

In each period the count rates for the first day of each 27-day interval, i.e., the 1st, 8th, 55th, etc., days, were averaged giving a rate called $R_1$. Similarly the second-day average $R_2$ was obtained by averaging the data for the 2nd, 29th, 56th, etc., days.

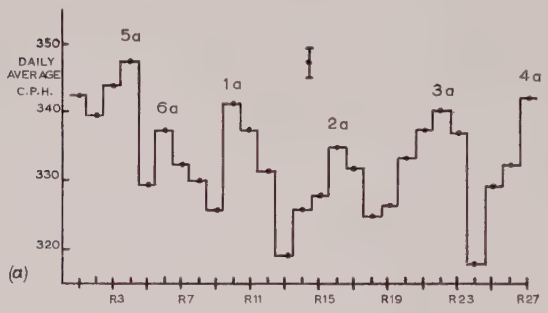
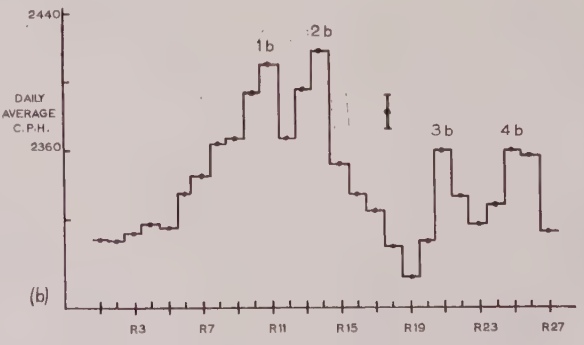



FIG. 3(a).—27-day variations of the period December 1956-April 1957. For explanation see text.

Figures 3a and 3b show plots of $R_1$ to $R_{27}$ for the two periods chosen. There are definite peaks in each curve indicating a tendency for disturbances to recur every 27 days.

In Figures 4a and 4b are plotted the actual daily rates during the periods concerned, with marks indicating the days corresponding to the various peaks of Figs 3a and 3b. A further analysis has shown that the maximum marked 2b is possibly a continuation of the maximum 2a, and 4b a continuation of 4a.

To reveal the mean diurnal variation, hourly count rates have been averaged for 100 consecutive days of the records (centred about January 1957) of pile A, and similarly 64 days (centred about June 1957) of pile B. The results are shown in Fig. 5a and b. It can be seen that, apart from a peak at 0400 hours. N.Z.M.T., in Fig. 5a, no statistically significant variation has been found.




(b).—27-day variations of the period May-July 1957.

## DISCUSSION OF RESULTS

Simpson, Fonger, and Wilcox (1952) have shown that there exists a unique correlation between solar-active regions and 27-day maxima.

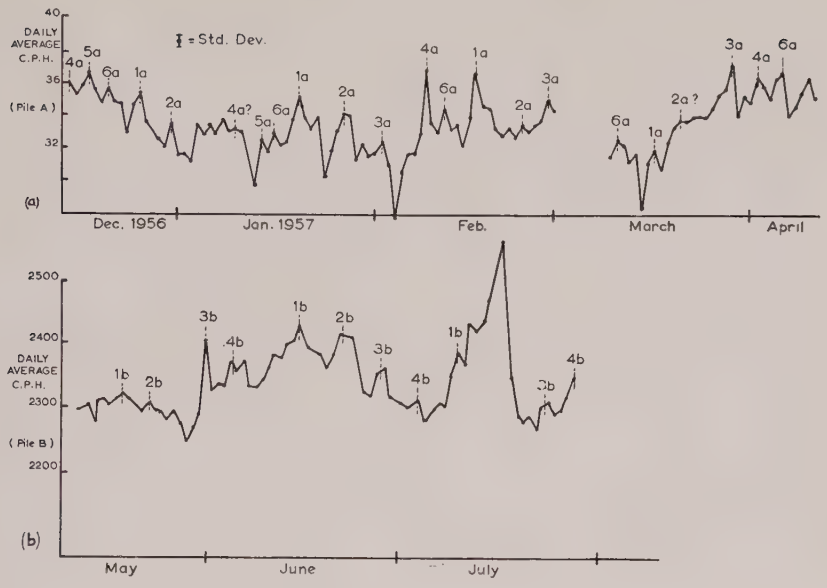



FIG. 4.—27-day maxima identified from Fig. 3a and 3b.

Meyer and Simpson (1954) have further demonstrated that 27-day maxima display an 11-year amplitude variation corresponding to a solar-active cycle.

However, a study of the days of this experiment on which maxima of the 27-day variations occurred showed that there were no increases in intensity at the impact zone times. From Fig. 3 it will be seen that the 27-day increase is of the order of 10% of the total counting rate. This large increase over a day would require an increase in cosmic ray intensity of more than 200% in the well defined 0400 hour impact zone (the most probable zone in these latitudes). Figure 6 which is a plot of mean hourly intensity for 6 days which display 27-day maxima, shows that no such increase is observed. Thus, these results, within their statistical variation, preclude the sun as the source of particles producing the maxima of 27-day variations, if such particles follow Lust's orbits.

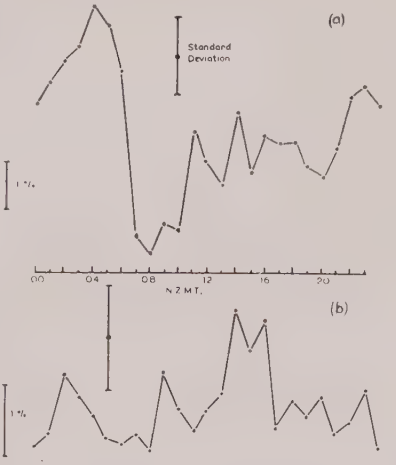



FIG. 5.—Averaged count-rates showing diurnal variations of the nucleonic component.

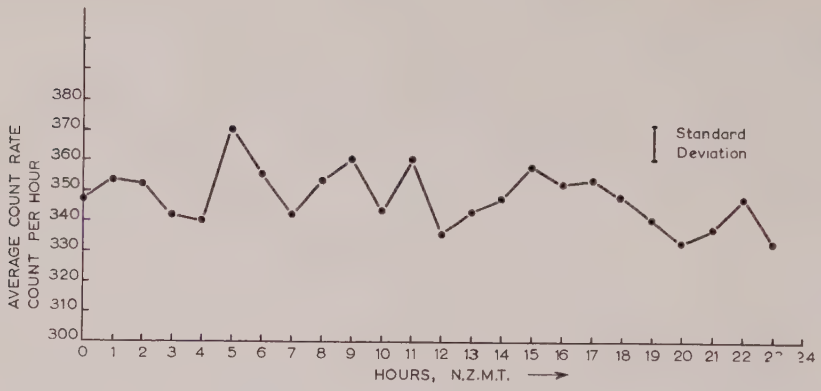



FIG. 6.—Averaged hourly count-rate for 6 days of 27-day maxima.

The above evidence tends to indicate that the form of the intensity curve of Fig. 4 is not produced by solar particle emission. It seems likely that the variation in cosmic ray intensity is better explained by a modulation effect of ionic clouds, with their associated magnetic fields, on a constant intensity of particles (Parker, 1956). In this view it is the minima rather than the maxima of the curve of Fig. 4 which should be examined for 27-day recurrence. Some support for this view is provided by the curve of Fig. 4(a) where the upper limit of intensity is fairly well defined, and could be the constant cosmic ray intensity of this region at this time, while the minima show a considerable scatter.

The daily analysis has indicated a significant peak at 0400 hours in Fig. 5a. This time corresponds to the most probable impact zone for Wellington (Lust, 1957). Although no other maxima in Fig. 5a or 5b are significant statistically, it is interesting to note that each curve displays an increase at about 1400 hours N.Z.M.T. This is in close agreement with the 1500 hours (local time) diurnal maximum found by Firor (1954) and which he has associated with an extra-terrestrial non-solar origin.

Further maxima in Fig. 5a are suggested at about 1100 hours and 2200 hours, and at 0200, 0900, and possibly 2000 hours in Fig. 5b. Allowing for the seasonal shift of impact zones (Lust, 1957) these maxima may represent the cumulative effect of a number of small solar flares. However, the appearance of all three zones in these latitudes would not be in complete harmony with Lust's theory.

## ACKNOWLEDGEMENTS

The author's sincerest thanks are due to the late Mr N. V. Ryder for his encouragement and advice in this work; also to Mr R. W. Humphrey for his valuable collaboration and assistance.

## REFERENCES

COCCONI, G.; COCCONI-TONGIORGI, V.; WIDGOFF, N., 1950: Cascade of Nucleonic Disintegrations Induced by Cosmic Radiation. *Phys. Rev. 79* : 768.

FIROR, J., 1954: Cosmic Radiation Intensity-time Variations and their Origin. 4. Increases Associated with Solar Flares. *Phys. Rev. 94* : 1017.

JORY, F. S., 1956: Selected Cosmic Ray Orbits in Earth's Magnetic Field. *Phys. Rev. 103* : 1068.

LUST, R., 1957: Impact Zones for Solar Cosmic-Ray Particles. *Phys. Rev. 105* : 1827.

MEYER, P.; SIMPSON, 1954: Changes in Amplitude of the 27-day Cosmic Radiation Intensity Variation with Solar Activity. *Phys. Rev. 96* : 1085.

MEYER, P.; PARKER, E.; SIMPSON, J., 1956: Solar Cosmic Rays of February, 1956 and their Propagation through Interplanetary Space. *Phys. Rev. 104* : 768.

PARKER, E. N., 1956: Modulation of Primary Cosmic Radiation Intensity. *Phys. Rev. 103* : 1518.

SIMPSON, J. A.; FONGER, W. H.; WILCOX, L., 1952: A Solar Component of the Primary Cosmic Radiation. *Phys. Rev. 85* : 366.

SIMPSON, J. A.; FONGER, W. H.; TREIMAN, S. B., 1953: Cosmic Radiation Intensity-time Variations and their Origin. 1. Neutron Intensity Variation Method and Meteorological Factors. *Phys. Rev. 90* : 934.

SIMPSON, J. A., January 1955: "Cosmic Ray Neutron Monitor Handbook." University of Chicago, Chicago.

SUDMAN, SEYMOUR, 1954: Report No. 39. Institute for Nuclear Studies, Chicago.

TREIMAN, S. B., 1952: Analysis of the Neucleonic Component Based on Neutron Latitude Variations. *Phys. Rev. 86* : 917.

WADA, MASEMI, 1957: S.C.R.I.V. Newsletter No. 2.57.

# NUTRITIONAL STUDIES OF *PHYTOPHTHORA CACTORUM* (LEB. AND COHN.) SCHROET.

## PART 2: INFLUENCE OF pH OF A CULTURE MEDIUM ON UTILIZATION OF SOME NITROGEN AND CARBON COMPOUNDS

By T. Christie, Cawthron Institute.

*(Received for publication, 2 June 1959)*


### *Summary*

Three nitrogen compounds, $Ca(NO_3)_2$, asparagine and $(NH_4)_2SO_4$, were tested as sources of nitrogen for growth by *Phytophthora cactorum* in a basal medium adjusted to pH levels between 3·0 and 9·0 with dextrose and sucrose as sources of carbon.

In the media with dextrose as the carbon source $Ca(NO_3)_2$ supported maximum growth at pH 6·0, asparagine at pH 5·0 and $(NH_4)_2SO_4$ at pH 6·0. With sucrose as the carbon source maximum growth with $Ca(NO_3)_2$ was made at pH 5·0, with asparagine at pH 7·0 and with $(NH_4)_2SO_4$ at pH 7·0.

In all media the fungus did not grow at pH 3·0. At pH 9·0 all three nitrogen compounds supported growth with dextrose as the carbon source. Only $Ca(NO_3)_2$ gave growth at this pH level with sucrose as the source of carbon.


### Introduction

In a previous study of the utilization of nitrogen and carbon compounds by a strain of *P. cactorum* isolated from a hop plant (Christie, 1958), it was found that the growth of the fungus in a synthetic medium appeared to vary according to the initial pH of the solution. To examine further this effect of pH three nitrogen compounds, calcium nitrate, asparagine and ammonium sulphate, were selected as sources of nitrogen and the growth of the fungus determined over a range of pH values from 3·0 to 9·0. Two sources of carbon, sucrose, and dextrose, were used with each of the above sources of nitrogen.

### Materials and Methods

Stock cultures of the fungus were maintained on potato-dextrose agar at room temperature.

A basal culture medium of the following composition was used: $Ca(NO_3)_2$, 3·80 g; $KH_2PO_4$, 2 g; KCl, 0·5 g; $MgSO_4.7H_2O$, 0·5 g; dextrose, 30 g; distilled water, 1000 ml; and thiamine hydrochloride, 25 p.p.m. All chemicals used were of standard analytical grade.

Asparagine and ammonium sulphate were substituted singly for calcium nitrate and dextrose for sucrose in the above medium in amounts sufficient to maintain the nitrogen and the carbon at the same level.

The cultures of the fungus were grown in 50 ml of the solution in 250 ml Erlenmeyer flasks. Each series was grown in five replicates. All flasks used were cleaned in a sulphuric acid-potassium dichromate solution and well washed with distilled water. All solutions were autoclaved at 15 lb pressure for 15 in.

Before inoculation of the flasks the pH of the solutions was adjusted by means of N/10 HCl and N/2 and N/10 NaOH, using a B.D.H. capillator, to pH values between 3·0 and 9·0. At the end of the growth period the pH of each series of solution was determined.

A standard inoculum measuring 3 mm square of the fungus growing on potato dextrose agar was used for each flask solution. After inoculation the flasks were placed in an incubator and maintained for 17 days at 23° C.

At the end of the growth period the mycelium from each flask was filtered on tared filter paper, well washed with distilled water and dried in an oven at 60° C for 24 hr. The amount of growth was determined by weighing the dried mycelium from each flask. The weights recorded represent the mean weight of the five replicates of each substance tested. The maximum standard error determination did not exceed ± 12 mg.

## Experimental Results

The growth of the fungus in the media with dextrose as the source of carbon is shown in Table 1 and with sucrose as the source of carbon in Table 2.

In all media at a pH level of 3·0 no growth was made by the fungus. With sucrose as the carbon substrate only $Ca(NO_3)_2$ as a nitrogen source yielded growth at pH 9·0. However, at this pH level with dextrose as the source of carbon all three nitrogen compounds supported growth.

Table 1.—Influence of pH on Utilization of Three Nitrogen Compounds by *P. cactorum* in a Basal Medium with Dextrose as the Carbon Source.

| | $Ca(NO_3)_2$ | | Asparagine | | $(NH_4)_2SO_4$ | |
|---|---|---|---|---|---|---|
| Initial pH of solution | Weight of mycelium (mg) | pH of solution at end of growth period | Weight of mycelium (mg) | pH of solution at end of growth period | Weight of mycelium (mg) | pH of solution at end of growth period |
| 3·0 | No growth | — | No growth | — | No growth | — |
| 4·0 | 127 | 4·2 | 141 | 4·2 | 6 | 3·8 |
| 5·0 | 155 | 5·0 | 151 | 5·2 | 18 | 4·8 |
| 6·0 | 171 | 5·2 | 130 | 5·2 | 24 | 4·8 |
| 7·0 | 110 | 5·2 | 94 | 5·2 | 16 | 5·6 |
| 8·0 | 74 | 5·4 | 71 | 5·4 | 11 | 6·2 |
| 9·0 | 16 | 5·4 | 33 | 6·0 | 10 | 6·2 |

TABLE 2.—Influence of pH on Utilization of Three Nitrogen Compounds by *P. cactorum* in a Basal Medium with Sucrose as the Carbon Source.

| | $Ca(NO_3)_2$ | | Asparagine | | $(NH_4)_2SO_4$ | |
|---|---|---|---|---|---|---|
| Initial pH of solution | Weight of mycelium (mg) | pH of solution at end of growth period | Weight of mycelium (mg) | pH of solution at end of growth period | Weight of mycelium (mg) | pH of solution at end of growth period |
| 3·0 | No growth | — | No growth | — | No growth | — |
| 4·0 | 17 | 3·8 | 65 | 5·2 | 11 | 5·0 |
| 5·0 | 190 | 5·0 | 85 | 5·2 | 28 | 5·0 |
| 6·0 | 166 | 5·2 | 85 | 5·2 | 34 | 5·2 |
| 7·0 | 100 | 5·2 | 117 | 5·2 | 42 | 5·2 |
| 8·0 | 92 | 5·6 | 114 | 6·0 | 29 | 6·4 |
| 9·0 | 40 | 5·6 | No growth | — | No growth | — |

Of the three sources of nitrogen tested $Ca(NO_3)_2$ yielded the best growth with better growth taking place in the media containing sucrose than in that with dextrose. The fungus made poor growth in the media with $(NH_4)_2SO_4$ as the nitrogen source, although growth was better with sucrose than with dextrose. Asparagine gave better growth in the acid media with dextrose than with sucrose; in the more alakaline media the opposite was the case.

The optimum growth of the fungus was made at different pH levels with the three compounds of nitrogen. In the media with sucrose $Ca(NO_3)_2$ supported maximum growth at pH 5·0; asparagine at pH 7·0 and $(NH_4)_2SO_4$ at pH 7·0. In the media with dextrose $Ca(NO_3)_2$ gave maximum growth at pH 6·0; asparagine at pH 5·0 and $(NH_4)_2SO_4$ at pH 6·0.

The variations of growth in this series of experiments indicate the importance in studies of this nature of taking into account the initial pH of the media before any comparative conclusions can be drawn of the ability of the fungus to utilize nitrogen and carbon compounds.

## REFERENCE

T CHRISTIE, 1958: *N.Z. J. Sci. 1*: 83-90.

# THE GROWTH OF TEREDO (*Bankia australis* Calman) IN OTAGO HARBOUR

By D. E. Hurley, New Zealand Oceanographic Institute, Department of Scientific and Industrial Research, Wellington

*(Received for publication, 24 April 1959)*


## *Summary*

Wooden test-blocks were used over a fourteen-month period at Portobello Marine Biological Station, Otago Harbour, to determine the incidence and growth-rate of "teredo" or "shipworm" (*Bankia australis* Calman). Analysis by radiography revealed no detectable teredo on one-month blocks throughout the period; it is considered that a preliminary period of immersion of one to two months in sea water is necessary before the blocks induce settlement of teredo. Detectable animals first showed up after two months' immersion and a moderately heavy infestation was visible at three months. A cessation of spawning is indicated for a month or two in mid-winter when harbour temperatures reached as low as 5·2°C; signs of new infestation appeared again in August. There is evidence that coatings of ascidans, algae, hydroids, and other fouling animals inhibit settling of teredo on blocks, and that ultimate size of teredo is greatly influenced by its population density.


## Introduction

Little published work is available on the growth and life-history of the teredo, *Bankia australis* Calman, in New Zealand waters. Brief accounts of borer infestation in New Zealand ports have been published in the series "Deterioration of Structures in Sea-Water" (D.S.I.R. [U.K.]) but except for one report by Mason (1920), they contain no biological information. Ralph and Hurley (1952) reported on growth rates in Port Nicholson (Wellington Harbour), as revealed by infestation of wooden test-blocks, and Carr (1953) has discussed the reistance of various timbers and preservatives to teredo in Auckland Harbour. Mason (1920) reported that teredo was absent from Otago Harbour, and attributed this to high pollution by Dunedin City sewage which was discharged in the harbour until 1916. The present findings disclose that *Bankia australis* does occur in Otago Harbour now.

The work reported here was carried out from October 1952 to December 1953 at Portobello Marine Biological Station, Otago Harbour (Fig. 1), and was planned to obtain information on settling and growth rates of marine fouling and boring organisms for comparison with that already obtained from Port Nicholson (Ralph and Hurley, 1952).

## Methods

Two series and types of test-blocks were used. The major series was of rimu blocks (*Dacrydium cupressinum*) arranged in pairs after the pattern illustrated in Ralph and Hurley (1952). From the work in Wellington Harbour it was found that 12 in. × 12 in. × 1 in. blocks

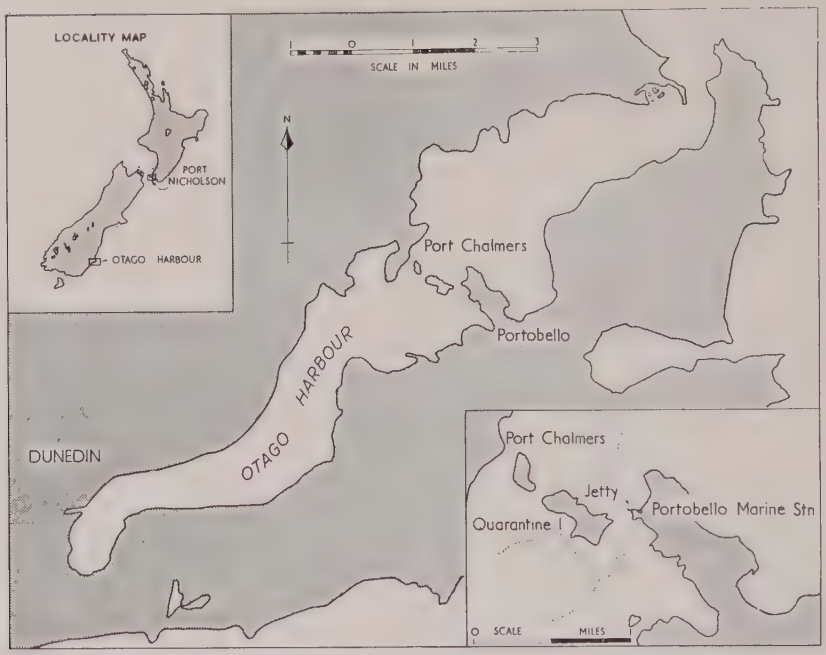



FIG. 1.—Locality map showing Port Nicholson (Wellington Harbour) and Otago Harbour; Portobello Marine Biological Station and Main Jetty.

involved long periods for examination and counting of organisms; it was therefore decided to use smaller blocks, 6 in. × 6 in. × $\frac{3}{4}$ in., thereby reducing the surface to about one-fifth. This considerably reduced the time needed for general examination, and allowed for more detailed examination while the blocks were in fresh condition, as well as making microscopic examination easier.

Twelve sets of paired rimu blocks ("first rimu series") were put down on October 20 1952, from the main jetty at the Portobello Marine Station, to provide a short- and a long-term series. The first block doubled as short- and long-term block for that month; thereafter, one long-term block was taken up each month and replaced by a short-term block which was removed after one month's immersion.

This should have resulted in information from 12 short- and 12 long-term blocks covering the period October 20 1952, to October 20 1953, but an unusually severe storm during mid-February 1953, resulted in four of the long-term blocks being lost with part of the jetty. Four replacement blocks were therefore put down in March so that the long-term blocks form two series—an eight-block series from October to May, and a four-block series ("second rimu series") put down in March and taken up from June to October, the first of these having been down 4 months and the last 8 months. This has made interpretation of the results rather more complicated, but has revealed valuable information about autumn and winter settling.

To provide information on hydroid settlement, a further series of short- and long-term blocks was put down in February 1953 and carried through until December 1953. This series has been extremely useful in extending information on teredo settlement obtained from the rimu blocks. These blocks were single pieces of Douglas Fir (*Pseudotsuga taxifolia*), 6 in. × 6 in. × ¾ in., suspended horizontally on a wire passed through a central hole and knotted immediately above and below the block. These blocks were more convenient to make and set in place but did not provide the variety of micro-ecological niches of the double blocks.

The Portobello Marine Station jetty is on the edge of the Portobello Channel (Fig. 1). The current here is relatively swift, but the site of the wharf is such that blocks suspended under it probably miss the full force of the current. Because of the absence of suitable wooden stringers, the blocks were individually suspended at intervals along a thick manila rope lashed between pilings; and the suspension wire was adjusted so that all blocks were at approximately the same level (1 ft below extreme low water, spring tide). Replacement of short-term blocks to the same level by one person from a dinghy, was often difficult, especially in unsatisfactory weather, but the differences in level resulting from uneven replacement and from gradual sag in the rope were only slight. A storm during mid-August 1953, caused a rope to break, and the loss of the July-August short-term rimu block. The rope was replaced on 27 August.

The teredo holes were counted after fouling growths had been recorded and removed. Blocks were labelled for radiography by tacks or small nails in their corners.

*Bankia* have a pair of calcareous bivalve shells anteriorly which are modified to assist in boring, and posteriorly a pair of calcareous pallets shaped like ears of wheat which are used for stopping the entrance when the fleshy siphon is withdrawn into the burrow. In addition, the animals line their burrows with a calcareous layer. Shells, pallets, and burrow lining show up in radiographs which thus provide relevant information which could otherwise be obtained only by splitting the blocks, an unsatisfactory procedure when blocks are heavily infested.

Usually, either pallet or siphon protrudes from the burrow. If the block has been out of water for some time, the animal contracts and these structures are withdrawn inside the burrow, but the entrance hole is usually visible.

## MEASUREMENT OF BANKIA

Measurement of *Bankia* from radiographs involves some difficulties, more so in 6 in. × 6 in. than in 12 in. × 12 in. blocks. Normally, the animals burrow along the grain of the wood as far as possible. In the smaller blocks, boring cannot proceed far before a change in direction is required. In a comparatively short time, burrows become doubled and trebled and areas where more than one animal has settled become exceedingly congested.

FIG. 2.—Radiograph of vertical test-block of first rimu series after six months' immersion (20 October 1952, to 22 April 1953). Pallets, shells, and surface layer burrows are clearly visible. The pallets resemble paired ears of wheat; the shells appear as paired crescentic or circular objects, sometimes separated but in most specimens overlapping. Striations down the centre of the block are caused by grain in the wood and are parallel to the surface layer of burrows. The mottled background is caused by convolutions in underlaying layers of burrows in the crowded block. Black circles in the bottom corners are numbering tacks.

This is shown in Fig. 2 where the impossibility of measuring burrow lengths accurately when this stage has been reached is demonstrated. An alternative was to measure pallet lengths instead of burrow lengths. In Fig. 3, pallet lengths of selected individuals plotted against burrow lengths, give reasonably valid comparative lengths, with 1 mm of pallet representing approximately 1 cm of total length (as indicated by burrow length). Pallet lengths have therefore been used in graphs of growth rates.

Occasionally the narrow stalks of the pallet end against the burrow wall in a position which masks the end of the stalk, and sometimes the pallet is not entirely in the horizontal plane and has been fore-shortened in the radiograph. As far as possible, pallets have been measured only where they are reasonably distinct and horizontal.

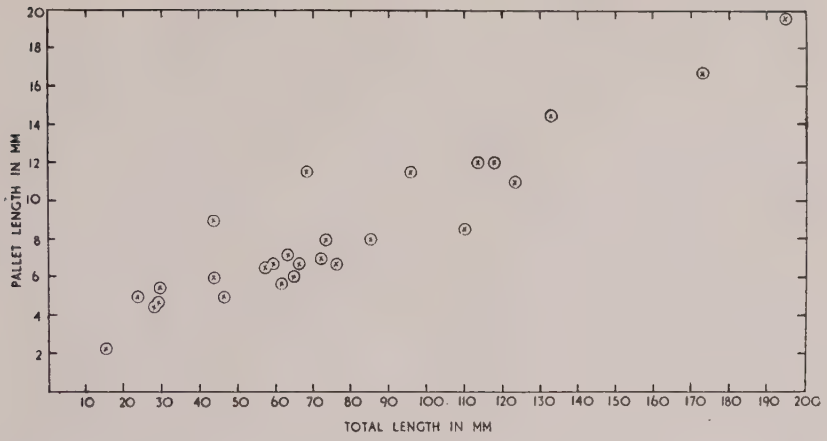



FIG. 3.—Pallet lengths of *Bankia australis* Calman plotted against total burrow lengths.

## TEMPERATURE

Temperature is a critical factor in the spawning of ship-worm. In tropical species, spawning may continue throughout the year; in colder-water species, there is evidence that spawning slackens and even ceases during winter

Sea-surface temperatures at Wellington and Portobello are compared in Figs. 4 and 5. The data given for Wellington are those of Ralph and Hurley (1952) and were recorded during 1949-50 at Te Aro salt-water baths at 9 a.m. daily. The Portobello readings are 9 a.m. records

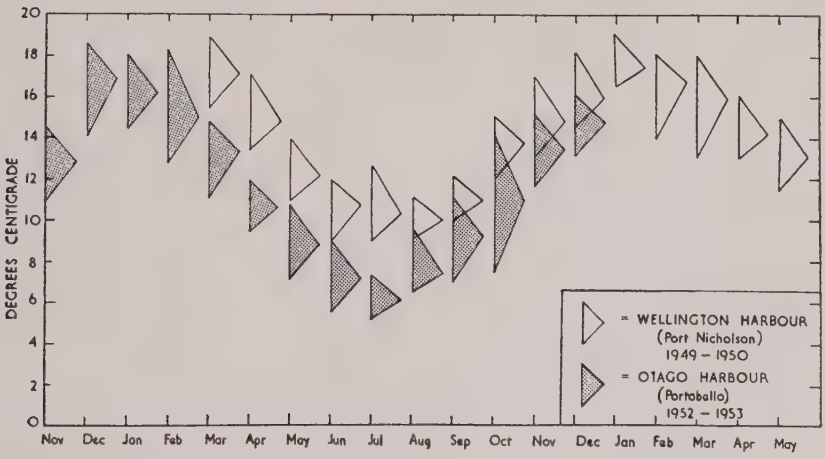

DEGREES CENTIGRADE
= WELLINGTON HARBOUR (Port Nicholson) 1949 – 1950
= OTAGO HARBOUR (Portobello) 1952 – 1953
Nov Dec Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec Jan Feb Mar Apr May

FIG. 4.—Monthly sea temperatures in Wellington and Otago Harbours measured at Te Aro Salt-water Baths and Portobello Marine Biological Station respectively. The upper point of the triangle represents the maximum temperature, the lower the minimum, and the third point the mean monthly temperature.

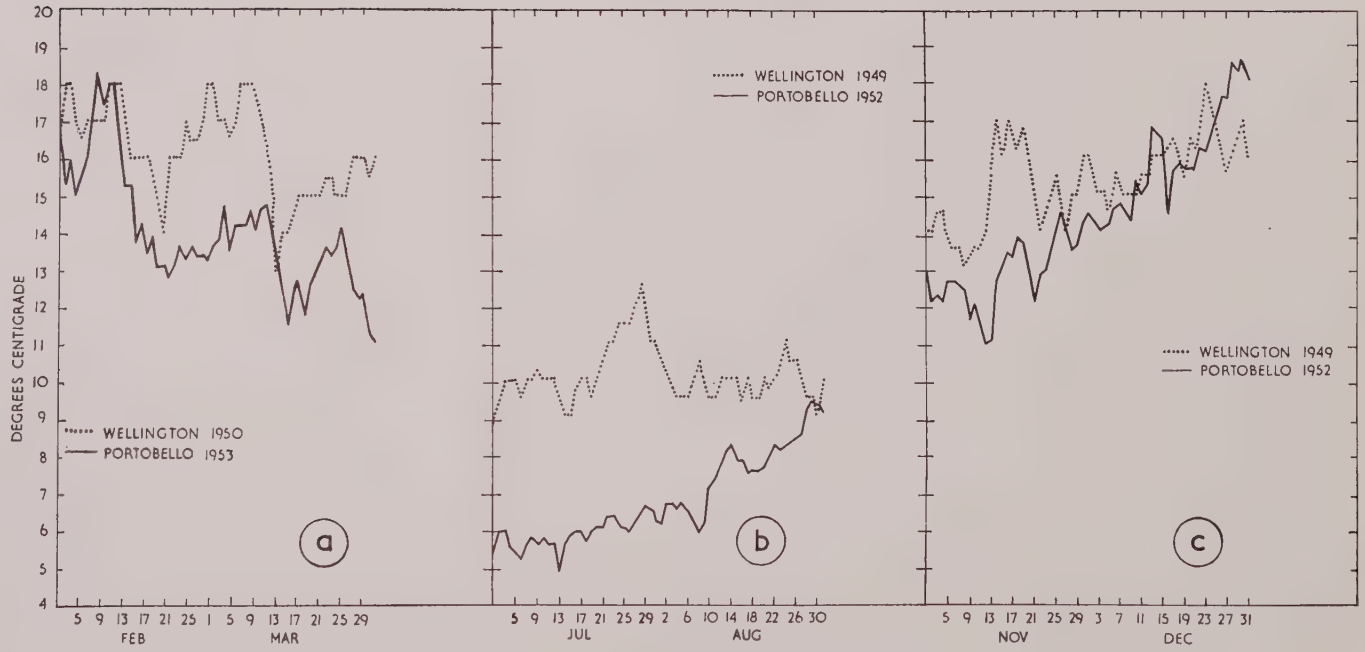



FIG. 5.—Comparison of daily sea temperatures between Wellington and Portobello showing (a) an earlier autumn fall at Portobello, (b) lower winter temperatures at Portobello, and (c) later spring rise at Portobello.

during 1952-53, from the end of the main jetty. More recent Wellington temperatures are given in Skerman (1958), but the earlier, although less accurate, temperatures have been used here for comparison with the (1949-50) Wellington teredo investigation.

Figure 4 uses a system similar to that evolved for Ralph and Hurley (1952) to summarize temperature data. The vertical base line of the triangle represents the range of temperature for the month, but the third point of the triangle is the monthly average temperature, not the temperature most frequently recorded for the month.

In Fig. 5, daily sea temperatures from Wellington and Portobello are compared for the months February-March, July-August, and November-December. These are the months of greatest temperature differences between the ports. In February-March the Portobello temperature falls away rapidly while the Wellington temperature remains relatively high; in July both ports reach their minimum, but in August the Portobello temperature rises rapidly to within a degree or less of Wellington temperatures; and in November-December Portobello temperature may even surpass the Wellington temperature. The striking similarity of the two curves is, however, purely coincidental since they represent different years.

The important features of the comparison are the rapid annual rise and fall in Portobello temperatures, with maximum temperature in both ports 18° C (in some years slightly higher in Wellington); the shorter period of maximum temperatures for Portobello (January-mid-February as against January-late March for Wellington); and the considerably lower Portobello minimum, approximately 4° C below Wellington.

Batham (1956) reports a minimum low temperature of 4·8 ° C on 13 July 1952 and 28 July 1954 for Portobello, whereas the lowest recorded by Skerman for Wellington was 6·7° C in the week July 7-12 1955. Earlier records of lower winter minima at Portobello (Thomson, 1905; Anderton, 1906) are open to question (Hurley and Burling, in press).

Otago Harbour is extremely shallow with large areas of sandbank above water at low tide. Thus, it is characterized by rapid heating and cooling of large areas of shallow water, and, in winter, freezing of salt spray along the foreshore and of ice on outside saltwater tanks have been noted.

Figure 6 compares daily air and sea temperatures for Portobello from mid-September to early December 1953. Over this period temperatures are gradually rising but there are several distinct falls in sea temperature, preceded in each instance by a more extreme drop in air temperature about 24 hours earlier. (See especially periods September 28-October 1; December 4-8.) The sea and air temperatures are very closely related. Batham (1956) noted that monthly average sea and air temperatures differed usually by less than 1° C, and that daily sea and air temperatures usually lay within 2° C of each other, the greatest difference noted being 6·9° C.

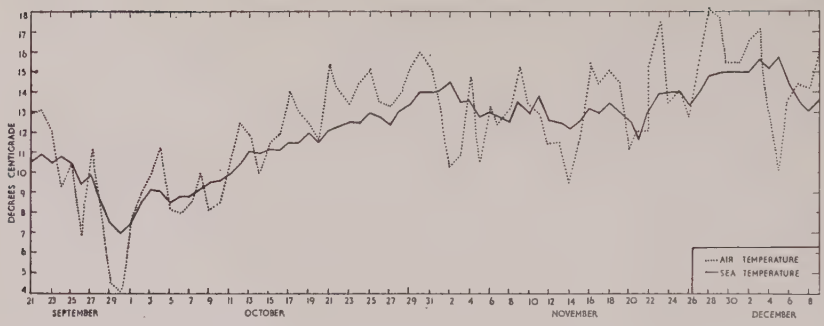



FIG. 6.—Daily air and sea temperatures at Portobello from late September to December 1953, showing rapid response of sea temperature to air temperature.

These temperatures are significant in regard to *Bankia*. Both harbours are suitable for year-round survival of *Bankia*, and Wellington is probably suitable for year-round spawning, but there is a suggestion, from evidence recorded below, that temperatures in Otago Harbour may fall below suitable spawning temperatures for a short period in mid-winter.

## LIFE-HISTORY OF TEREDO

The life-history of the teredo is known in outline, mostly from species of the genus *Teredo*. *Bankia* species are less well-known; some work has been done in Canada on *Bankia setacea* (Quayle, 1956a, 1856b; Tabata and LeBrasseur, 1958) and other northern species; almost nothing is known about the biology of *Bankia australis*.

In *Bankia setacea* spermatozoa and ova are shed into the open water separately. The larva grows to about 0·01 of an inch in length in the free-swimming stage; it then settles and is able to bury itself completely in wood within 24 hours (Quayle, 1956b). The life-history of *Teredo* is similar in so far as it buries itself completely in a matter of hours after settling (Lane, 1955). It may be assumed that this also happens with *Bankia australis*.

It is not known if *Bankia* can prolong larval free-living life after it has reached this size (0·01 in.) if no suitable settling place has then been found, but the planktonic larval stage may last up to a month (Quayle, 1956b).

According to Miljutina (1959), metamorphosis of *Teredo navalis* from settlement of the pelagic larva to adult mollusc takes about ten days which can be divided into two periods. During the first 1½-2 days, the larva attaches itself by its byssus gland and positions itself for burrowing. In the second period, from the 8th to the 10th day, the "veliconcha" larva transforms itself into a young mollusc (differing in organization from the adult), develops rasping teeth, and commences boring.

This is in accordance with what would be deduced as the most effective larval stage for a marine boring animal; the duration of the pelagic

larva would be relatively long to allow maximum possibility of finding suitable wood for settling, but the time between settling and burrowing would be as short as possible and need only be delayed long enough for the animal to find the best burrowing spot on the preferred surface, and to develop its burrowing mouthparts. Radiographs should thus record the presence of *Bankia* juveniles which have settled a few days previously.

## SPAWNING AND SETTLING

The incidence of infestation of long-term blocks (Table 1) confirms evidence from short-term blocks that no settling takes places within the first month of immersion and little within the second. (No teredo appeared on any short-term block.) However, the set on the third-month blocks (Fig. 7) is as high as that on the eighth-month block.

TABLE 1.—Number of *Bankia australis* Calman Found Monthly in Pairs of Long-term Blocks at Portobello 1952-53.

| | N | D | J | F | M | A | M | J | J | A | S | O | N | D |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| First rimu Series | 0 | 2 | 25 | 21 | 20 | 29 | 19 | 25 | — | — | — | — | — | — |
| Second rimu Series | — | — | — | — | — | — | — | — | 0 | 0 | 1 | 2 | — | — |
| Fir series | — | — | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 4 | 3 |

Since the interval between settling and burrowing is only a matter of hours, and there is evidence from the following year's results that spawning was taking place in October when the blocks were first put down, it is likely that one- to two-month's immersion is necessary to "condition" the blocks before they become favourable for settlement. This conditioning may be a matter of water absorption, of leaching out of resin and toxins, of softening of fibres, of accumulation of a sufficient bacterial and diatom primary fouling film to attract the teredo larva, or of combinations of these factors. Lane (1955) notes that "lignins and other materials that bind the cellulose fibres of the wood together must be so modified that the larva is able to insinuate itself into the substance of the wood."

Wellington results (Ralph and Hurley, 1952) showed a similar delay in settling and absence of infestation of short-term blocks.

Numbers settling in one pair of blocks in Portobello during each month from January to May vary from 19 to 29; this variation does not seem greatly significant and is probably due to normal random settling and such modifying factors as variable incidence of other fouling organisms from block to block. The teredo already present in the block are, in themselves, unlikely to prevent further settlement.

The second rimu series and the Douglas Fir series of blocks are useful in defining spawning times over the winter. The first rimu series indi-

FIG. 7.—Horizontal test-block of first rimu series after three months' immersion (20 October 1952, to 20 January 1953). The position of the shells in the centre of the burrows is due to shrinkage of the animals between time of lifting of blocks and radiography.

cated that spawning and settlement was taking place from at least late October onwards. The second rimu series suggested that spawning commenced much earlier, at the latest from August onwards, and this was confirmed by limited settling on the fir blocks about the same time. By August, the temperature was already on the upswing after the July low of approximately 5·2° C. Individuals of 6 mm pallet were present on the May block of the first rimu series so that spawning continued through from August to April. Field notes record that *Bankia* larvae were observed on March blocks. If there is a critical temperature, below which spawning does not take place, and if spawning occurs in August, as is suggested, then it appears from temperature records for June, July, and August (Fig. 2) that cessation of spawning is likely only for July and early-August. In any event, it would seem to be only a very short period of the year, possibly less than two months. In a some-

what similar temperature regime in British Columbia, Quayle (1956b) found that breeding could occur in *Bankia setacea* at any time of the year.

The fir blocks placed down in January showed no settling until August. Allowing two months for conditioning, it would be expected that settling would show up on March or April blocks. A probable explanation of the fact that it did not is that shielding of the block by a blanket of ascidians, algae, hydroid, sponge, and bryozoan protected the blocks from autumn settling which, in a period of declining temperatures, would be less prolific than spring or summer settling. *Bankia* larvae may also be actively fed upon by ascidians, polychaetes, and other fouling animals. When *Bankia* did penetrate the covering, numbers were low even in December, although the few animals that did settle grew rapidly. The possibility that the fir blocks require longer conditioning is not borne out by the Wellington work where fir was also used.

## EFFECT OF FOULING ON SETTLING

One of the features of the test-blocks, and of Otago Harbour generally, is the abundance of colonial and solitary ascidians. There are a considerable number of species common at Portobello and many turned up on the test-blocks, e.g. *Botryllus schlosseri, Botrylloides leachi, Corella eumyota, Didemnum candidum, Diplosoma macdonaldi, Asterocarpa cerea, Ascidia aspersa, Didemnum psammatodes, and Pyura pachydermatina.* They were first found to be abundant on the January blocks and from then on they covered up to 90% of some blocks, tending to be absent or restricted only on the muddy upper surface of the horizontal block. Colonial species, in particular *Didemnum candidum*, formed a carpet which could be peeled off the block to reveal a clean surface underneath. This growth was such that, once the blanket covering of ascidian was established, it must have seriously impeded the settlement of *Bankia,* as it is unlikely that the *Bankia* would settle on and burrow through the ascidian layer to reach the underlying wood.

On the fir blocks, ascidian covering was well established before conditioning was likely to have been adequate for teredo settling. There was prolific hydroid and ascidian growth on the February block; and ascidian, algae, and some hydroid on March and April blocks. This blanket covering of fouling organisms is likely to have excluded teredo from heavy invasion. Ascidians were thick before teredo began settling, and incidence of settling was low throughout the fir series, only three animals being found in the final block (Fig. 8) which had been immersed for twelve months.

The second rimu series was put down in March, a period of low fouling intensity, and these blocks did not acquire a heavy fouling coating until quite late in the following series. The fact that teredo invasion on this series was also slow is evidence, allowing for one to two months' conditioning, for cessation of spawning in mid-winter.

The upper horizontal block was more commonly covered with mud than fouling organisms and therefore settling of teredo might have been expected on that surface, especially since they are reported to prefer silt

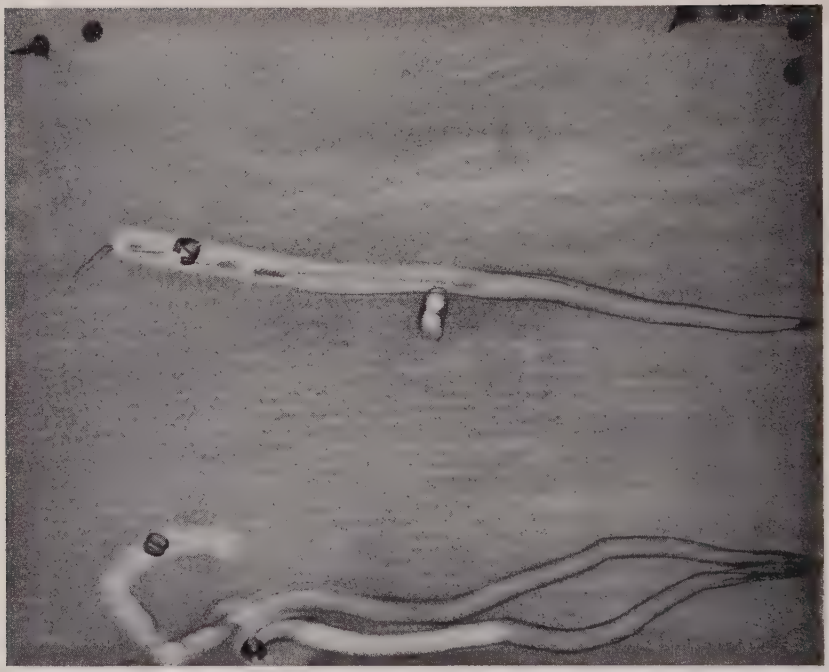


FIG. 8.—Horizontal test-block of fir series after 12 months' immersion (17 December 1952, to 16 December 1953). Burrows clearly follow grain of wood.

surfaces for settling (Doochin and Walton Smith, 1951), but preference for such a surface was not obvious.

It is possible that other factors such as current velocity or the disturbances of a stormy winter operated at Portobello to modify the set of *Bankia*. Doochin and Walton Smith, for example, found evidence that *Teredo pedicellata* was prevented from settling by currents of 1·4 to 1·8 knots, velocities which are certainly reached at Portobello. In a regular tidal cycle, however, these velocities are not continuous, and at Portobello tidal and storm effects would probably be secondary factors by comparison with fouling and temperature.

## GROWTH RATES

The spread of pallet lengths for each month is shown in Fig. 9—this may be referred to the graph of pallet length against total burrow length (Fig. 3).

Figure 10 shows average pallet length plotted against months. This curve reveals the remarkably quick growth of the organism from initial burrowing to approximately 12 mm pallet length (100-120 mm minimum body length) and then the curve flattens off. This flattening off may be due to any of at least four possible causes. It may be an anomaly arising from difficulties in measuring pallet length and by differential growth of pallet and total length. (The evidence is against

this latter, cf. Fig. 3.) It may represent slackening or cessation of growth after attainment of sexual maturity. It may be caused by recruitment of juveniles in later monthly settling depressing the average of pallet lengths. This almost certainly accounts for the April-May depression of the graph, but is not likely to be significant in the overall picture. Finally, it may be due to a forced halt on further growth due to over-crowding of the test-blocks. It is possibly significant that each fir block is inhabited by only a few individuals, and growth of pallets is much greater than in the rimu series.

Upper limits of growth are set by crowding and may or may not coincide with adult maturity, which in *Bankia setacea* has been reported within 4 months after settling (Quayle, 1956b). In a crowded population (Fig. 11), animals in a very short time have nowhere to turn unless they cross and penetrate existing burrows. In fact, teredo are not known to do this; they stop short before touching other burrows. Figure 11 shows that the animals actually turn and reverse their burrows half a centimetre before reaching the edge of a block, and the changes in direction form a remarkably straight line. Obviously, they can detect the edge of the block by some means when more than 5 mm from it, and this almost certainly applies to detection of other burrows.

This indicates the restriction inherent in using 6 in. × 6 in. blocks for teredo measurement. The animals very quickly find that they have

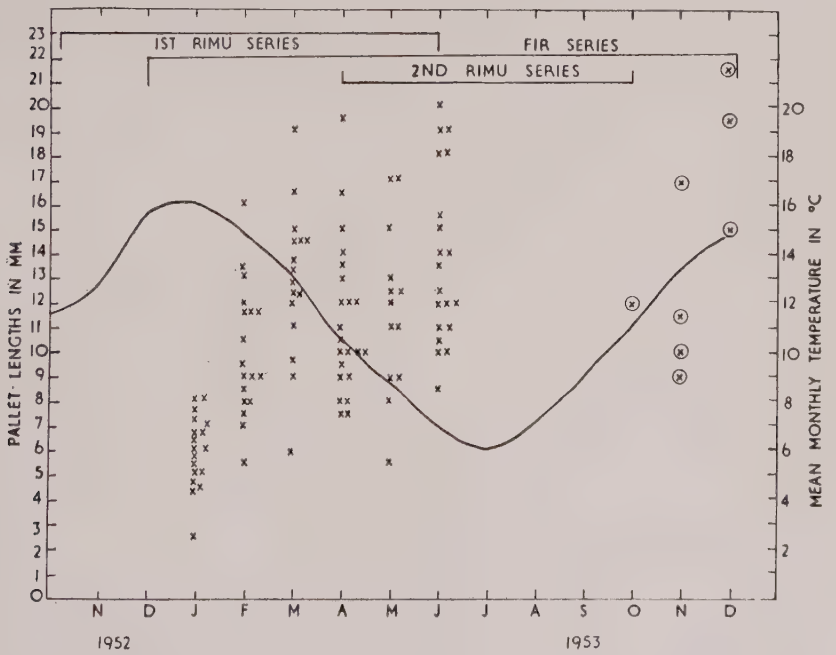



FIG. 9.—Individual pallet lengths of *Bankia australis* Calman at Portobello showing monthly growth measurements and monthly average sea temperatures. No pallets were measurable for the second rimu series of test-blocks.

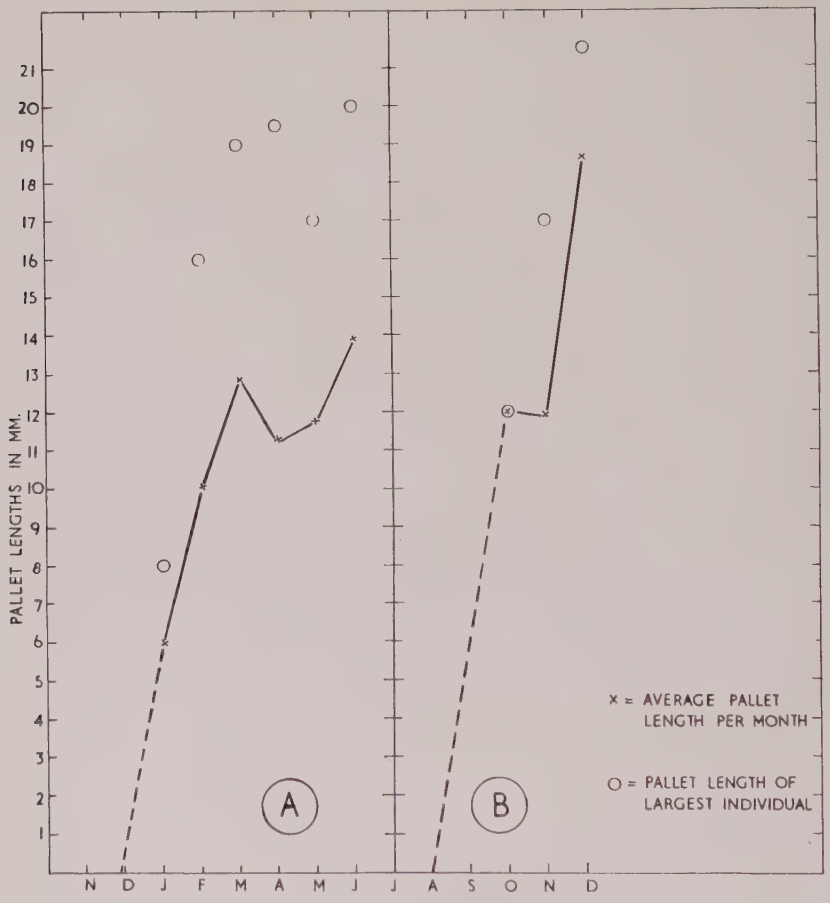



FIG. 10.—Average pallet length and pallet lengths of largest individuals of *Bankia australis* Calman at Portobello plotted against monthly occurrence (1952-53). A represents first rimu series; B represents fir series. (Extrapolated to presumed month of settling.)

grown into a cul-de-sac as the block becomes crowded, and growth then stops. "The standard procedure appears to be to develop a calcareous rounded cap over the anterior end of the borer. This seals off the burrow and effectively terminates growth *and the continued life of the animal*." (Lane, 1955, the present author's italics.) Although there is no sign of such caps in Fig. 11, it is evident that crowding allows little prospect of further burrowing.

There is no obvious sign in these blocks of "indigenous spawning" causing re-infestation in considerable numbers, such as noted in Wellington (Ralph and Hurley, 1952), and also with *Bankia setacea* by Tabata and LeBrasseur (1958) in British Columbia. This may also be due to protection by fouling organisms.

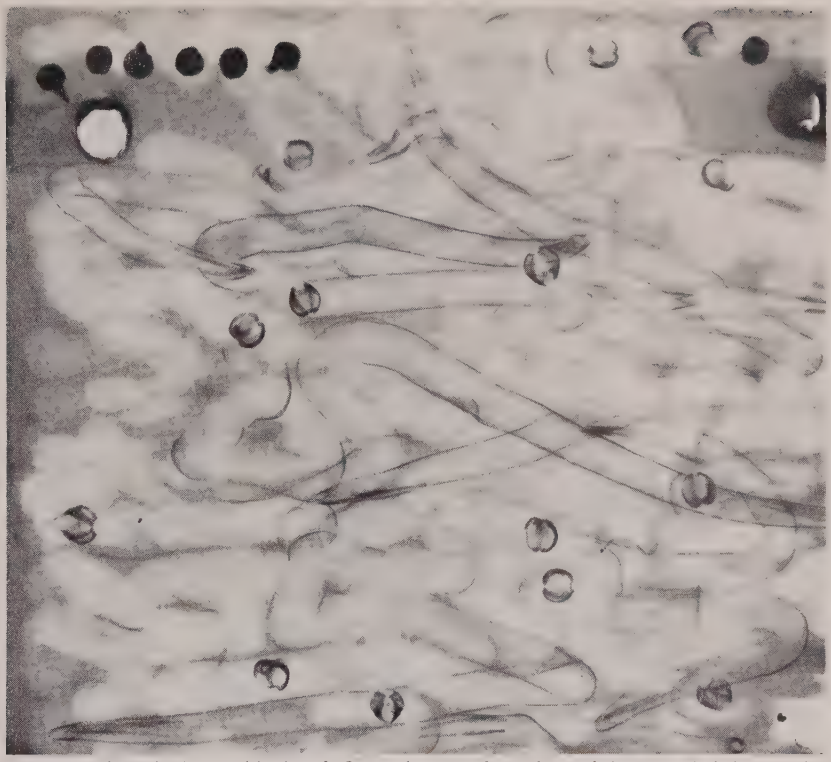


FIG. 11.—Vertical test-block of first rimu series after eight months' immersion (20 October 1952, to 18 June 1953). The burrows on the left margin stop short and turn back before reaching the edge of the block.

## CONCLUSIONS

There is evidence that spawning and settling of *Bankia* in Otago Harbour occur throughout most of the year, ceasing for at most about three months of the year and possibly less in winter when temperatures reach as low as 5° C, but re-commencing in August when the temperature is again rising and may be as high as 10° C. Compared with conditions in Wellington Harbour, settling is not particularly heavy at any time of the year. This may be related to current velocity as well as lower winter temperature and shorter periods of maximum temperature; it may also be related to greater modification of settling by fouling "blankets", attributable in part to the heavy ascidian component found in Otago Harbour.

Growth is extremely rapid to pallet length of about 12 mm (total length 120 mm) in 6 in. × 6 in. blocks but then slackens off rapidly, probably due to overcrowding rather than to achievement of total adult length. In uncrowded conditions, the fir blocks indicate that pallet lengths of 20 mm (total length approximately 200 mm) may be quickly reached in 6 in. × 6 in. blocks.

Blocks require one to two months' conditioning by immersion in sea water before *Bankia australis* will commence settling.

## Acknowledgements

The field work for this study was carried out at Portobello Marine Biological Station during tenure of a Nuffield Research Grant. Miss P. M. Ralph of Victoria University of Wellington generously permitted use of information gained from test-blocks placed at her request. Contact prints of radiographs were made in D.S.I.R. photographic laboratories by Mr S. N. Beatus. To various individuals who helped at different times with preparation and placing of blocks, in particular Mr R. Stark of Portobello, and to those responsible for the series of radiographs without which this work would not have been possible, grateful thanks are expressed. Mr H. R. Orman of New Zealand Forest Service confirmed identification of woods used.

## References

Anderton, T., 1906: Observations on New Zealand Fishes, &c., made at Portobello Marine Fish-Hatchery. *Trans. N.Z. Inst. 39* : 477-96, pls. 17-20

Batham, E. J., 1956: Ecology of Southern New Zealand Sheltered Rocky Shore. *Trans. roy. Soc. N.Z. 84 (2)* : 447-65, pls. 29-31, 9 text-figs.

Carr, D. R., 1953: Marine Borers in Timber Structures. *N.Z. Engng 8 (11)* : 389-98, figs 1-6, 5 tables.

Department of Scientific and Industrial Research [U.K.] : "Deterioration of Timber, Metal, and Concrete Structures Exposed to the Action of Sea Water". Reports of the Committee of the Institution of Civil Engineers, 1920-1951. H.M.S.O., London.

Doochin, H.; Walton Smith, F. G., 1951: Marine Boring and Fouling in relation to Velocity of Water Currents. *Bull. Mar. Sci. Gulf & Caribbean, 1 (3)* : 196-208, figs 1-4, 3 tables. (Also *Contr. No. 60, Mar. Lab., Univ. Miami.*)

Hurley, D. E.; Burling, R. W., in press: The Ecological Significance of Some Early Sea Temperature Records from Otago Harbour. *N.Z. J. Geol. Geophys. 2* :

Lane, C. E., 1955: Recent Biological Studies on *Teredo*—A Marine Wood-boring Mollusc. *Sci. Mon. N.Y. 80 (5)* : 286-92, figs 1-4. (Also *Contr. No. 129, Mar. Lab., Univ. Miami.*)

Mason, J. B., 1920: Otago Harbour, N.Z., Deterioration of Structures in Sea-Water. *Rep. Comm. Struct. Sea-Wat., Lond. 1* : 204-5.

Miljutina, N. A., 1959: Observations on *Teredo navalis* during its Settling on and Boring into the Wood. *Zool. Zh. 38 (4)* : 520-36, figs 1-10.

Quayle, D. B., 1956a: Growth of the British Columbia Shipworm. *Pacific Biol. Sta. Nanaimo B.C., Prog. Rep., 105* : 3-5, figs 1-2.

———, 1956b: The British Columbia Shipworm. *Rep. Fish. Dep. B.C. 1955* : K.92-K.104, figs 1-15.

Ralph, P. M.; Hurley, D. E., 1952: The Settling and Growth of Wharf-pile Fauna in Port Nicholson, Wellington, New Zealand. *Vict. Univ. [N.Z.] Zool. Publ. 19* : 1-22, figs 1-4, 2 tables.

Skerman, T. M., 1958: Seasonal Variations in Sea-water Surface Temperatures within New Zealand Harbours. *N.Z. J. Geol. Geophys. 1 (1)* : 197-218, figs 1-2, 9 tables.

Tabata, S.; LeBrasseur, 1958: Sea Water Intrusion into the Fraser River and its Relation to the Incidence of Shipworms in Steveston Cannery Basin. *J. Fish. Res. Bd. Can. 15 (1)* : 91-113, figs 1-14, 4 tables.

Thomson, G. M., 1905: The Portobello Marine Fish-Hatchery and Biological Station. *Trans. N.Z. Inst., 83* : 529-558, pls 55-59.

# AN EXPERIMENTAL STUDY OF FACTORS INDUCING AGGREGATION IN MARINE PLANKTON

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## *Summary*

Two continuous plankton sampling traverses were made across Port Nicholson (Wellington Harbour), using a plankton pump fitted with auxiliary equipment for recording continuously temperature and salinity. The hose intake was maintained at a constant depth of 10 metres and 100 plankton samples were taken, each representing a volume of 200 litres and a horizontal distance of 115 metres. Three species of zooplankton were counted, *Paracalanus parvus, Podon polyphemoides,* and *Elminius modestus* nauplii. Multiple regression and covariance analysis were used to interpret the results. The temperature-salinity record indicates that 7 distinct zones of water were traversed, plus two extensive zones of turbulent mixing. Within each zone, *Paracalanus* is positively correlated to salinity, which is consistent with its known preference for oceanic water, but a slight negative correlation to temperature cannot be explained. In the pooled data for all zones, *Elminius* nauplii are strongly correlated with higher temperature and lower salinity, both conditions being more favourable to the liberation of larvae by the parent barnacles. Positive correlations are found between *Paracalanus* and nauplii, and between *Podon* and nauplii. All species show pronounced correlation between adjacent sample counts (autocorrelation), but this can mainly be attributed to external factors, and is not therefore evidence of gregarious behaviour (contagion). Relationships shown are sufficient to account for a substantial proportion of the excess variance which cannot be attributed to random distribution. From the evidence obtained here, there is some reason to believe that physical inhomogeneities in the open ocean may be of sufficient magnitude to influence the small-scale spatial pattern of plankton distribution.


## Introduction

This experiment is one of a series designed to reveal some of the factors influencing the pattern of spatial distribution of marine plankton in a horizontal plane. Particular attention is paid to the effect of variations in physical properties of the water. Some of the considerations leading to this work have previously been discussed briefly (Cassie, 1957).

It is now well known and generally accepted that many, if not most, plankton organisms show a marked departure from randomness in their horizontal distribution, even when samples are taken at relatively close intervals. More commonly non-randomness is in the direction of over-dispersion (aggregation), a condition which may usually be detected by comparing the variance of sample counts with the mean. When the distribution is Poisson (random), these two statistics will be approximately equal, but when over-dispersion is present the variance

will be greater than the mean. Tests of significance of this difference are available, but will be superfluous with the present data, since over-dispersion is too pronounced to be open to doubt.

The term "contagion" has frequently been used in ecological literature as a synonym of over-dispersion. It is proposed that "contagion" be reserved to describe the special case where over-dispersion is attributable to biological attraction between individuals of the same species rather than to a common seeking of favourable niches in the external environment. (Conversely, negative contagion may be employed as a special case of under-dispersion, where the variance is less than the mean, although the present paper is not concerned with this phenomenon.) It will, in fact, be shown that certain apparent cases of contagion may be traced to external causes, provided the appropriate information is available.

While the causes of over-dispersion are undoubtedly manifold, it was considered desirable to investigate the magnitude of the contribution made by inhomogeneity of the environment, and to weight this contribution against other primarily biological factors. The two properties, temperature and salinity, are chosen as a measure of inhomogeneity because, beside being biologically significant, they are virtually independent of the organisms themselves (as compared with oxygen, carbon dioxide, nutrient content, all of which may be significantly changed by the plankton population). They are at the same time variable in space, but conservative in time (as compared with solar radiation, which may change more rapidly than the plankton can react). In addition to their biological significance, the combined temperature and salinity values may serve as an index of the origin and past history of the water they describe.

This experiment was carried out in the enclosed inshore waters of Port Nicholson (Wellington Harbour), so that inhomogeneities would be large enough for both the properties themselves and their effects to be readily measured. While a coastal plankton population will not be entirely comparable with an offshore population, it seems likely that the information gained will be at least a guide to the study of oceanic plankton.

An experiment of similar nature has been carried out by Barnes and Marshall (1951), in this case with the primary object of fitting suitable mathematical models to the frequency distribution of sample counts. However, with one set of samples, these workers have also recorded temperature and salinity and have shown graphically that correlations exist between these properties and species counts. Although the number of samples (20 in effect) is too small to make a detailed analysis, the results of their investigation were sufficiently convincing to encourage the development of the technique used in the present experiment.

## Field Procedure

The sampling apparatus used has been previously described (Cassie, 1958). It consists of a centrifugal pump, hose, and auxiliary instru-

ments, capable of drawing water from shallow depths, filtering out the plankton, and recording continuously the salinity and temperature. For this experiment, the apparatus was mounted on a 40 ft motor launch. The outboard end of the 40 ft hose ($1\frac{1}{2}$ in. internal diameter) was secured to a towing warp which was held down in the water by a 50 lb bronze cable depressor (Reed and Stewart, 1949). The hose intake was a 2 ft length of $1\frac{1}{2}$ in. brass pipe, the mouth of which projected about 6 in. in front of the warp.

The course taken by the vessel is indicated in Fig. 1. Once the run was commenced, the ship's motor was maintained at a constant speed, which was as slow as possible, consistent with maintaining steerage way. The average speed was 3·6 knots, although the speed over the ground varied from about $2\frac{1}{2}$ to 5 knots under the influence of tidal currents. The vessel was maintained on a straight course on each of three legs of the run by keeping two shore marks in line. Three-point sextant fixes were taken at approximately 5 min. intervals and records were also kept of the compass heading of the ship. From this information, it was possible to make an estimated of surface currents encountered.

Sampling was continuous, the filters being changed at 1 min. intervals, a total of 100 samples being taken, 50 on the eastward and 50 on the westward run, with an interval of 1 hr between the two runs.

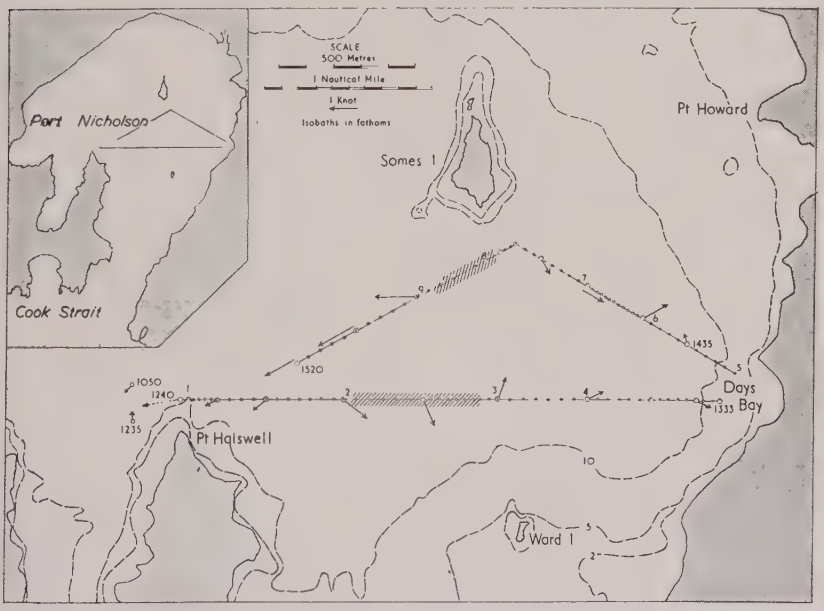


FIG. 1.—Chart showing course of ship and sample positions. Large open circles: three-point sextant fixes. Small black and open circles indicate beginning and end of samples. Zones 1 to 9 numbered in sequence at commencement of each zone.

The average distance covered in 1 min. was 115 metres, a figure which may be taken as representing a fairly constant horizontal column of water traversed (as opposed to a more variable distance in relation to the land). The pumping rate of 200 litres per minute was also maintained constant, so that the sample taken may be regarded as representing a horizontal cylinder of water 4·7 cm in diameter, which is only slightly greater than the intake diameter of the hose (3·8 cm). This arrangement of the underwater sampling head seems to approach closely to the ideal for sampling the smaller plankton. Not only are there no bridles or other obstacles preceding the intake, but the water has a virtually uninterrupted flow through the receiving aperture, without the pressure wave preceding a conventional net. While some of the more active pelagic organisms may still avoid capture, it has been found that even small fish may be taken on occasion and pass through the pump without visible damage.

On the day of the experiment (28 July 1958), the wind was a light north-westerly, with 3/10 cumulus cloud and slight seas. Predicted high tide was at 14·42 hr and sampling was from 12·40 hr to 13·30 hr (west to east) and 14·30 hr to 15·20 hr (east to west).

## PHYSICAL CHARACTERISTICS OF THE WATER

Surface currents, estimated from ground speed and ship's heading, are indicated by arrows in Fig. 1, the lengths of the shafts being proportioned to the speeds. Absence of an arrow indicates still water, except at the apex of the triangle, where the information was considered unreliable. The estimates are approximate, but are reliable to the extent of showing general features of the circulation. This may be compared with the ebb-tide circulation described by Brodie (1958), who indicates that the main southward-moving stream occupies the western two-third of the channel, passing round both sides of Somes Island, but running almost entirely to the west of Ward Island. A narrow counter-current runs northward along the eastern shore. The general pattern shown in Fig. 1 is consistent with Brodie's diagram, although an exact comparison can not be made because sampling in the present instance was carried out about high tide, when neither flood nor an ebb pattern would be fully developed.

The temperature and salinity record is shown at the top of Fig. 2. Average values for each 1 min. interval have been estimated by placing a transparent straight-edge along the original record, so that equal areas are enclosed on either side by the recorded trace. Heavy vertical bars indicate the maximum range within the minute. The two runs (west to east and east to west) are divided into nine zones (separated by vertical lines in Fig. 2) on the basis of the *T-S* diagram, which will be discussed below. In most zones, the temperature and salinity range is small compared with overall variation, but two zones (2 and 8) present a more violent fluctuation. The original record suggests that in both cases the actual range was even greater still, but that the change was frequently so rapid (up to 5 oscillations per minute) that the re-

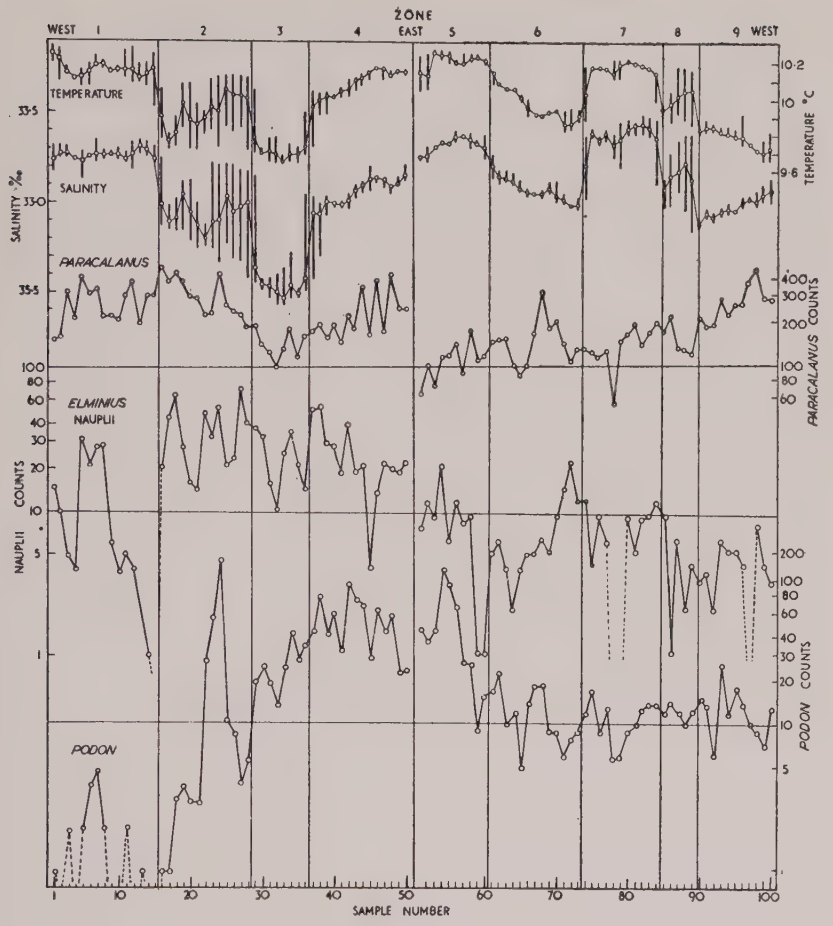


FIG. 2.—Graphical summary of temperature, salinity, and plankton data (plankton on logarithmic scale).

corder, printing at 5 sec. intervals on any one trace, did not always mark the extremities of the swing. Both zones appear to represent regions of turbulent mixing between the zones adjacent on either side. Zone 2 appears to be associated with a counter-clockwise eddy, as indicated by the reversal of current direction, which was noted by the helmsman as an abrupt change of set corresponding with the eastern boundary of the zone. Similar mixing regions, though of less than 1 min. duration, occur at other points of temperature-salinity change.

Temperature and salinity have a high positive correlation ($r_{TS} = 0{\cdot}86$), which is apparent in the $T$-$S$ (temperature-salinity) diagram (Fig. 3).

The regression of $S$ on $T$ may be expressed as:

$$\hat{S} = 22{\cdot}00 + 1{\cdot}151\,T$$

This may be extrapolated to give $T = 11{\cdot}0°$ C, $S = 34{\cdot}7‰$ (standard error = 0·36%), which agrees well with the Cook Strait values at the time: 11° C and 35‰ approximately. On the other hand, the temperature of the Hutt River immediately above the tidal part of the estuary was 8° C, corresponding in the regression to a salinity of 31·2‰. This suggests that the low temperature, low salinity element in the samples may be regarded as resident harbour water, originally a mixture of river and ocean water, but considerably modified by evaporation and other agencies. The high temperature, high salinity element comes from Cook Strait water, unmodified, except by dilution. Owing to the continuous movement of tides, the mixing process between the two types of water is turbulent, and violent fluctuations in properties, rather than gentle gradients, are the general rule.

In Fig. 3, the mean temperature and salinity values for each minute are plotted on a *T*-*S* diagram. From this presentation, it is possible to

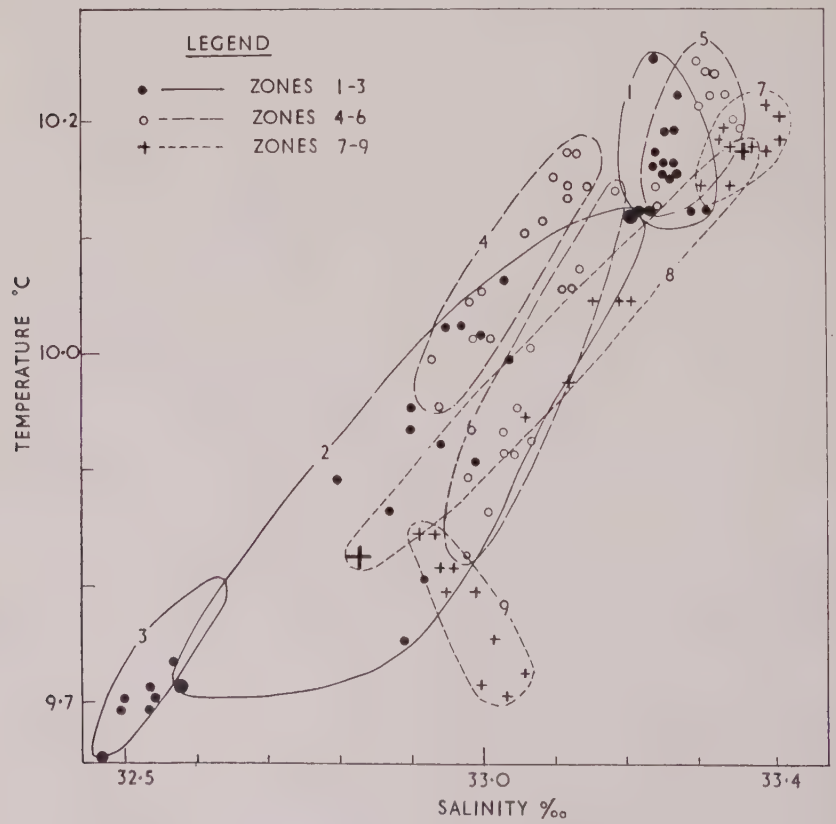


FIG. 3.—*T*-*S* diagram. Small symbols: mean temperature and salinity for each sample. Large symbols: maximum and minimum values for zones 2 and 8.

distinguish seven water "zones", each with its own distinctive combinuation of temperature and salinity, plus the two mixing zones previously described. The nine zones are numbered in the order in which they were encountered (see also Figs 1 and 2). In 2 and 8, two additional points (larger symbols) have been plotted to indicate the maximum and minimum $T$-$S$ combinations. Both mixing zones present a complete range of properties intermediate between those of their nearest neighbours.

Zones 1, 5, and 7 coincide fairly closely in the figure, suggesting some affinities, a matter which will be further discussed in connection with the plankton populations.

## THE PLANKTON

The plankton was mixed with a fairly large quantity of organic debris which rendered sorting difficult, and for this reason the phytoplankton and some of the less abundant zooplankton species, which might otherwise have been considered, have not been counted, as the time involved did not seem warranted by the information anticipated. The following three species have been recorded:

*Paracalanus* parvus (Claus) (Copepoda)
*Podon polyphemoides* Leuckart (Cladocera)
*Elminius modestus* Darwin (Cirripedia); stage V and VI nauplii (Knight-Jones and Waugh, 1949).

The numbers per sample of these three species are shown on a logarithmic scale in Fig. 2. It will be seen that there is no obvious relationship between these counts and the temperature-salinity curves, either in the form of direct numerical correlation, or as changes in abundance at zone boundaries. Such relationships, if they exist, must be sought in a more detailed statistical analysis.

In the text and tables, the following symbols and statistical terms will be used:

$C$ = *Paracalanus*, sample count
$P$ = *Podon*, sample count
$N$ = nauplii of *Elminius*, sample count
$T$ = temperature (° C)
$S$ = Salinity (‰)
$t, s, t', s'$ see text
$\bar{x}$ = mean
$s$ = standard deviation (also in equations 4 and 5 to indicate a salinity increment. The distinction will be obvious)
$s^2$ = variance
$n$ = number of samples
$k$ = number of variables in regression or correlation
d.f = degrees of freedom
$\wedge$ (circumflex) indicates predicted value of a variable
$c, d$, see text

$r$ = total or partial correlation coefficient
$R$ = multiple correlation coefficient
† = possibly significant ($P = 0{\cdot}1$ to $0{\cdot}05$)
* = probably significant ($P = 0{\cdot}05$ to $0{\cdot}01$)
** = significant ($P = 0{\cdot}01$ to $0{\cdot}001$)
*** = highly significant ($P = 0{\cdot}001$)

Correlation coefficients will be read thus:

$r_{CT}$ = Total correlation, $C$ to $T$
$r_{NP.CTS}$ = Partial correlation, $N$ to $P$, independent of $C$, $T$, and $S$
$R_{CTS}$ = Multiple correlation, $C$ to $T$ and $S$
$R_{CTS.PN}$ = Partial multiple correlation, $C$ to $T$ and $S$, independent of $P$ and $N$

Table 1 gives the means, variances, and two measures of dispersion, $c$ and $d$ for the three species. In each case, it is obvious from the great excess of $s^2$ over $\bar{x}$ that over-dispersion is highly significant.

$c$ is derived from the equation:

$$c = (s^2 - \bar{x})/\bar{x}^2$$

TABLE 1.—Means, Variances, and Coefficients of Dispersion.

| *Species* | $\bar{x}$ | $s^2$ | $c$ | $d$ |
|---|---|---|---|---|
| *Paracalanus* (pooled) ..... | 209 | 8861 | 0·20 | 0·977 |
| *Paracalanus* (within zones) | | 4938 | 0·11 | 0·958 |
| *Podon* (pooled) ..... ..... | 22·4 | 718 | 1·39 | 0·969 |
| *Podon* (within zones) ..... | | 699 | 1·35 | 0·978 |
| Nauplii (pooled) ..... ..... | 14·0 | 195 | 0·92 | 0·929 |
| Nauplii within zones) ..... | | 108 | 0·48 | 0·870 |

This statistic is a convenient measure of the magnitude of over-dispersion. It has an advantage over the more commonly used coefficient if dispersion ($s^2/\bar{x}$) in that it is not correlated with the mean, and thus has some validity in comparing populations with different means. On the other hand, the same population will not necessarily have the same $c$ for different patterns of sampling, or different sizes of samples. This implies that $c$ is dependent not only on the numerical, but also on the spatial magnitude of aggregations, in which case it could only be expected to be stable for a constant pattern of sampling. For finite values of $n$, limiting values are $n - 1/\bar{x}$ (maximum over-dispersion) and $-1/\bar{x}$ (maximum under-dispersion). For a Poisson distribution, $c = 0$ (although a zero value is not necessarily an exhaustive test for randomness).

$d$ is a measure of the excess variance above that expected to arise by chance.

Two value of $s^2$, $c$, and $d$ are given for each species. The "pooled" values are computed from all samples combined, and are the estimates which would normally be used, in the absence of further information. "Within zones" values are obtained by partitioning the squares of deviations from the mean into two components, one due to differences in density between the populations of the nine zones, and the other due to variations within the zones themselves. (A comparable analysis of variance is carried out on the logarithms of sample counts in Table 3.)

For *Podon*, the within zones variance is little different from the pooled variance, but for the other two species variance is reduced to about half its previous value. Even so, the reduction in $d$ is not great.

It will be seen from Table 1 that in every case the proportion of non-random variance is 87% or more. The statistic $d$ is comparable with $R^2$, the square of the coefficient of multiple correlation, which is a measure of the proportion of the variance of a dependent variable which is attributable to regression on independent variables. While $d$ and $R^2$ can not be exactly equated, it will be expected that, if over-dispersion is to be entirely accounted for by regression on external factors, $R^2$ will be required to be fairly large, probably 0·9 or even higher.

## CORRELATIONS WITH TEMPERATURE AND SALINITY

For the purposes of this section of the analysis, the plankton counts have been transformed to logarithms. This expedient serves a dual purpose. Firstly, it sufficiently fulfils the requirements for a valid analysis of variance which have been discussed in some detail by Barnes (1952). While other (and more complex) transformations are available, which may be slightly more satisfactory on theoretical grounds, the slight gain in information does not appear to justify the very much heavier computation which would be involved. Secondly, it has been found that when plankton numbers are correlated to physical variables, the coefficient of correlation is almost invariably larger after the log. transformation. This suggests that the relationship is a geometric one—i.e., that the influence of a given increment of temperature or salinity may be predicted as a multiplication or division of plankton numbers rather than as an arithmetic addition or subtraction.

Owing to the presence of nine different water zones, it is desirable that any comparison between plankton and physical properties should distinguish between these zones, since differences in plankton populations are as likely to be related to the origin and past history of the zones as to the direct influence of their present physical properties.

Table 2 gives means and standard deviations of temperature, salinity, and log. species counts. It might be expected from Fig. 2 that the populations of zones 1, 5, and 7 would have some features in common, that they would be rather different from zone 3, and that the remaining

TABLE 2.—Summary of Means and Standard Deviations.

| Zone | $n$ | Temperature | | Salinity | | Log. *Paracalanus* | | Log. Nauplii | | Log. *Podon* | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | $\bar{x}$ | $s$ | $\bar{x}$ | $s$ | $\bar{x}$ | $s$ | $\bar{x}$ | $s$ | $\bar{x}$ | $s$ |
| 1 | 15 | 10·17 | 0·04 | 32·70 | 0·02 | 2·43 | 0·13 | 0·79 | 0·54 | $\bar{1}$·98 | 0·50 |
| 2 | 13 | 9·94 | 0·09 | 32·38 | 0·07 | 2·43 | 0·14 | 1·35 | 0·35 | 0·83 | 0·64 |
| 3 | 8 | 9·72 | 0·04 | 32·49 | 0·05 | 2·15 | 0·10 | 1·34 | 0·20 | 1·40 | 0·16 |
| 5 | 14 | 10·09 | 0·07 | 32·49 | 0·07 | 2·35 | 0·15 | 1·33 | 0·28 | 1·68 | 0·20 |
| 4 | 10 | 10·21 | 0·04 | 33·76 | 0·04 | 2·04 | 0·13 | 0·78 | 0·44 | 1·59 | 0·35 |
| 6 | 13 | 9·97 | 0·09 | 33·51 | 0·06 | 2·16 | 0·15 | 0·80 | 0·27 | 1·05 | 0·20 |
| 7 | 11 | 10·17 | 0·05 | 33·82 | 0·04 | 2·13 | 0·16 | 0·61 | 0·62 | 1·03 | 0·15 |
| 8 | 5 | 10·01 | 0·04 | 33·58 | 0·05 | 2·18 | 0·11 | 0·53 | 0·38 | 1·08 | 0·05 |
| 9 | 11 | 9·79 | 0·05 | 33·41 | 0·05 | 2·43 | 0·11 | 0·53 | 0·32 | 1·08 | 0·18 |
| Pooled means ..... ..... | | 10·02 | 0·17 | 33·53 | 0·23 | 2·28 | 0·20 | 0·92 | 0·51 | 1·03 | 0·63 |
| Within zones means ..... | | | 0·06 | | 0·05 | | 0·14 | | 0·40 | | 0·35 |

TABLE 3 (see Appendix).—Analysis of Variance of Log. (Species Count) Between Zones.

| Species | Source of variation | Sum of squares | d.f. | Mean square | $F$ |
|---|---|---|---|---|---|
| *Paracalanus* | Deviation between zone means | 2·0953 | 8 | 0·2619 | 14*** |
| | Deviation from mean within zones | 1·6755 | 91 | 0·0184 | |
| *Elminius* nauplii | Deviation between zone means | 10·3518 | 8 | 2·1294 | 13*** |
| | Deviation from mean within zones | 14·7518 | 91 | 0·1621 | |
| *Podon* | Deviation between zone means | 27·3739 | 8 | 3·4218 | 28*** |
| | Deviation from mean within zones | 11·1884 | 91 | 0·1229 | |

sections would be intermediate in character. This is not borne out by the table. Nor do the populations of zones 2 and 8 have any greater range of variation, as might have been anticipated from the wider range of physical properties. Analysis of variance for each of the three species (Table 3) shows highly significant differences between the zone means, but Bartlett's ($\chi^2$) test shows no significant inhomogeneities between the variances. Thus it appears that the zones contain distinct populations (in the numerical sense), perhaps owing to their separate origins, but that there is no simple relationship to the degree of dilution of oceanic by harbour water.

Table 4 summarizes partial and multiple correlation coefficients of species to $T$ and $S$, both for all data pooled, and within zones. (Owing to the high correlation between $T$ and $S$ already mentioned, there is little to be gained by examining total correlations to either of these properties separately.)

In the pooled data, both *Podon* and *Elminius* nauplii show positive correlations with temperature and negative with salinity. The nauplii correlation is highly significant, and there is little doubt of its reality,

TABLE 4.—Correlation Coefficients, Species to Temperature and Salinity.

| | Partial | | Multiple | |
|---|---|---|---|---|
| | $r_{YT.S}$ | $r_{YS.T}$ | $R_{YTS}$ | d.f. |
| Pooled: | | | | |
| *Paracalanus* | — | — | 0·07 | 97 |
| *Podon* | 0·19 | —0·28* | 0·30** | |
| Nauplii | 0·33*** | —0·47*** | 0·50*** | |
| Within zones: | | | | |
| *Paracalanus* | —0·21 | 0·33** | 0·33** | 73 |
| *Podon* | — | — | 0·15 | |
| Nauplii | —0·10 | —0·13 | 0·27* | |

but the *Podon* correlation is relatively weak. The relationship is reversed for *Paracalanus*, which is positive to salinity and negative to temperature, shows no "pooled" correlation, but reaches significance in the "within zones" analysis. The temperature correlation is suspect, not quite reaching the "probably significant" level. However, some support may be given to its validity by the fact that the partial correlation to salinity ($R_{cs.T} = 0{\cdot}33^{**}$) is appreciably greater than the total correlation ($R_{cs} = 0{\cdot}26^{*}$).

The two contrasting types of correlation may now be considered in more detail.

### *Paracalanus*

In the case of *Paracalanus*, three further questions arise: Are the regressions homogenous between zones? Does the elimination of variance due to regression reduce the variance between zones? Do the variances remain homogeneous? The same three questions apply to the two possible cases—regression on salinity alone, and multiple regression on temperature and salinity. Table 5 gives abbreviated details of an analysis of covariance of *Paralacalanus* with salinity within zones. Owing to the small number of samples in each zone, the individual correlation coefficients differ considerably. There is, however, a preponderance of positive signs, three reaching possible or probable significance, while the only one of any magnitude in the negative direction is for section 8, with only 3 degrees of freedom. In the analysis of variance, the mean square for variation between zones is still highly significant and slightly larger than the corresponding value in Table 3, indicating that the zone populations have an individuality quite independent of salinity effects. The mean square for the variation between regressions of individual zones is not significant, thus giving no reason to suspect that the influence of salinity differs between zones. Bartlett's test for homogeneity of variance gives $\chi^2 = 6{\cdot}45$ (8 degrees of freedom) as compared with 4·10 for the same data unadjusted for regression (Table 3). However, probability of a larger $\chi^2$ occurring by change is still greater than 0·5. Thus it may be assumed that salinity has had no significant effect on the relative variability on the zone populations.

Table 6 is an analysis of covariance with $S$ and $T$. The partial correlation coefficients are again variable, but reasonably consistent, with a predominance of negative values for temperature and positive for salinity.

The tests of significance from the analysis of variance do not differ greatly from those obtained with the single regression on salinity. The mean square for variation between zones is again slightly increased, but there is no evidence of any variation in regression between zones. (Since the "between regressions" mean square is not significant, it is not necessary to distinguish between the temperature and salinity effects—see Appendix). Variances remain homogenous, with $\chi^2 = 4{\cdot}35$, which is lower than for the single regression, and thus lends

TABLE 5 (see Appendix).—Analysis of Covariance, *Paracalanus* with Salinity, Between Zones.

| Zone / Source of variation | $r_{cs}$ | Sum of squares | d.f. | Mean square | |
|---|---|---|---|---|---|
| 1 | —0·20 | 0·2304 | 13 | 0·0177 | |
| 2 | —0·00 | 0·2235 | 11 | 0·0203 | |
| 3 | 0·74* | 0·0322 | 6 | 0·0054 | |
| 4 | 0·46† | 0·2313 | 12 | 0·0193 | |
| 5 | 0·56 | 0·1083 | 8 | 0·0135 | |
| 6 | 0·00 | 0·2784 | 11 | 0·0253 | |
| 7 | 0·63† | 0·1456 | 9 | 0·0162 | |
| 8 | —0·54 | 0·0324 | 3 | 0·0108 | |
| 9 | 0·67 | 0·0690 | 9 | 0·0077 | |
| Total deviations from individual zone regressions | | 1·3511(1) | 82 | 0·0165 | |
| Deviations from common regression within zones | 0·26* | 1·5625(2) | 90 | 0·0174 | |
| Total deviations from regression | —0·09 | 3·7417(3) | 98 | | |
| Analysis of variance between zones: | | | | | *F* |
| Between zones, independent of regression (1–2) | | 2·1782 | 8 | 0·2723 | 16*** |
| Between regressions of individual zones (2–1) | | 0·2124 | 8 | 0·0266 | 1·6 |
| Deviations from individual zone regressions (1) | | 1·3511 | 82 | 0·0165 | |

TABLE 6 (see Appendix).—Analysis of Covariance, *Paracalanus* with Temperature and Salinity.

| Zone / Source of variation | $r_{CT.S}$ | $r_{CS.T}$ | $r_{CTS}$ | Sum of squares | d.f. | Mean square | |
|---|---|---|---|---|---|---|---|
| 1 | —0·55† | —0·33 | 0·57 | 0·1618 | 12 | 0·0135 | |
| 2 | —0·10 | 0·07 | 0·10 | 0·2213 | 10 | 0·0221 | |
| 3 | —0·79* | 0·86* | 0·90* | 0·0130 | 5 | 0·0026 | |
| 4 | 0·22 | —0·05 | 0·50 | 0·2206 | 11 | 0·0201 | |
| 5 | 0·13 | 0·52 | 0·57 | 0·1064 | 7 | 0·0152 | |
| 6 | 0·48 | —0·46 | 0·48 | 0·2143 | 10 | 0·0214 | |
| 7 | 0·44 | 0·67* | 0·72 | 0·1172 | 8 | 0·0147 | |
| 8 | —0·82 | 0·42 | 0·88 | 0·0104 | 2 | 0·0052 | |
| 9 | —0·61† | —0·08 | 0·80* | 0·0436 | 8 | 0·0055 | |
| | | | | 1·1086(1) | 73 | 0·0152 | |
| Total deviations from individual zone regressions | | | | | | | |
| Deviations from common regressions within zones | —0·21† | 0·33** | 0·33** | 1·4936(2) | 89 | 0·0168 | |
| Total deviations from regression | — | — | 0·07 | 3·7523(3) | 97 | | |
| Analysis of variance between zones: | | | | | | | *F* |
| Between zones independent of regression (3–2) | | | | 2·2586 | 8 | 0·2823 | 19*** |
| Between regressions of individual zones (deviation due to temperature and salinity combined) (2–1) | | | | 0·3850 | 16 | 0·0241 | 1·6 |
| Deviations from individual zone regressions (1) | | | | 1·1087 | 73 | 0·0152 | |

some support to the validity of the temperature correlation. There is, however, little to choose between the single and double regression, since the gain in information from adding temperature is small. Thus, although the temperature regression will be retained in the following discussion, its reality is rather more open to doubt than in the case of salinity.

Expressed as a regression quation, the "within zones" *Paracalanus* $T$-$S$ relationship becomes:

$$\log \hat{C} = a - 0{\cdot}80\ T + 1{\cdot}14\ S \qquad \ldots\ldots (1)$$

where $a$ is a constant for any one zone.
This equation may be expressed in the form:

$$\hat{C} = A \times 10^{(-0{\cdot}80T\ +\ 1{\cdot}14S)}\ (A = \text{antilog}\ a) \qquad \ldots\ldots (2)$$

or:

$$\hat{C}_{t's'} = C_0(0{\cdot}16^{t'}\ 14^{s'}) \qquad \ldots\ldots (3)$$

where $C_0$ is the known number of *Paracalanus* per sample at $T°$ C, $S‰$ salinity; $C_{t's'}$ is the predicted number per sample at $(T + t')°$ C, $(S + s')‰$ salinity.

This implies that, within any one zone, and under the conditions of this experiment, the number of *Paracalanus* may be expected to decrease by a factor of 0·16 for an increment of 1° C and to increase by a factor of 14 for an increment of 1‰ salinity. Since no one zone has a variation of this magnitude, it is more realistic to employ smaller increments, say, 0·1° C and 0·1‰. The appropriate equation then becomes:

$$\hat{C}_{ts} = C_0(0{\cdot}83^{t}\ 1{\cdot}30^{s}) \qquad \ldots\ldots (4)$$

where $t$, $s$ are the equivalents of $t'$, $s'$, but are expressed in tenths of the previous units.

As the above information was obtained under one restricted set of circumstances, caution is necessary in drawing any general ecological conclusion. However, the relationship suggests a species whose preferred habitat is in relatively cold water of normal oceanic salinity. While able to tolerate warmer, less saline water, the individual organism will, within the limits of its swimming powers, tend to seek the most congenial microclimate. In any discrete body of water (of which a "zone" is a cross-section), the mean population will be a function of the past history of the water, including its geographic origin, the availability of food organisms, and abundance of predators. Distribution within the zone will be determined—at least, in part—by the pattern of temperature and salinity. It will be noted also that, since these properties are positively correlated, but opposed in their influence on

*Paracalanus*, it is not surprising that the partial correlations, which are in any case small, are not evident in the graphical presentation of Fig. 3.

The positive correlation with salinity is consistent with the known distribution of the species, and preference for oceanic waters. Kramer, 1894, reports that *Paracalanus parvus* is common in Hauraki Gulf (near Auckland), but only an occasional visitor to the Waitemata Harbour, a relatively enclosed and less saline arm of the Gulf. Port Nicholson, which opens more directly to the open sea, is more frequently invaded by this species. Bary (1959) uses this species as an indicator of northern Subantarctic water in the New Zealand region, which is consistent with a preference for colder waters, at least by the local population. On the other hand, the geographic distribution of *Paracalanus parvus* extends from tropical to circumpolar seas, and there is no evidence of a local acclimatization to cold, since Cook Strait, from which the harbour population was presumably derived, though approaching its coldest temperature in July, is still warmer than the harbour. It is perhaps possible that differential vertical migration takes place, induced by specific gravity rather than temperature, in which case low temperature will operate in the same sense as high salinity. In the absence of further information, it would seem that the temperature relationship must remain unexplained.

### *Elminius nauplii*

The highly significant partial correlations seen in the pooled data for nauplii (Table 3) are reduced to insignificance in the within zones analysis, so that it is preferable to consider the pooled data as an entity. There is, however, a highly significant difference between the zone means, as shown by the analysis of variance (Table 3). The contribution of regression to the difference between zone populations may be assessed by an analysis of covariance on temperature and salinity producing the analysis of variance independent of regression in Table 7. In contrast to *Paracalanus*, the "between zones" mean square is very much reduced, though still highly significant. Thus temperature and salinity may be considered to be substantial, though not the only, factors in determining the populations of the zones.

Table 7.—Analysis of Variance Independent of Regression on Temperature and Salinity for *Elminius* Nauplii, and *Podon*.

| Species | Source of variation | Sum of squares | d.f. | Mean square | *F* |
|---|---|---|---|---|---|
| *Elminius* ..... | Between zones | 5·1655 | 8 | 0·6457 | 4·2*** |
| | Within zones | 13·6998 | 89 | 0·1539 | |
| *Podon* ..... ..... | Between zones | 27·4681 | 8 | 3·4335 | 30*** |
| | Within zones | 10·1803 | 89 | 0·1144 | |

In order to demonstrate graphically the partial regression on salinity, $S$ and log $N$ have been replotted (Fig. 4) with $N$ adjusted for partial regression on $T$ to a constant temperature of 10° C. The negative correlation then becomes apparent on inspection. The following is the appropriate regression equation, expressing the influence of increments of 0·1 units $T$ and $S$ (*cf.* equation 4 for *Paracalanus*):

$$\hat{N}_{ts} = N_0 \ (1{\cdot}50^{t} \ 0{\cdot}63^{s}) \qquad \ldots\ldots (5)$$

The partial regressions on temperature and salinity are appreciably larger than for *Paracalanus,* and in this case both are significant at the ($P = 0{\cdot}001$) level.

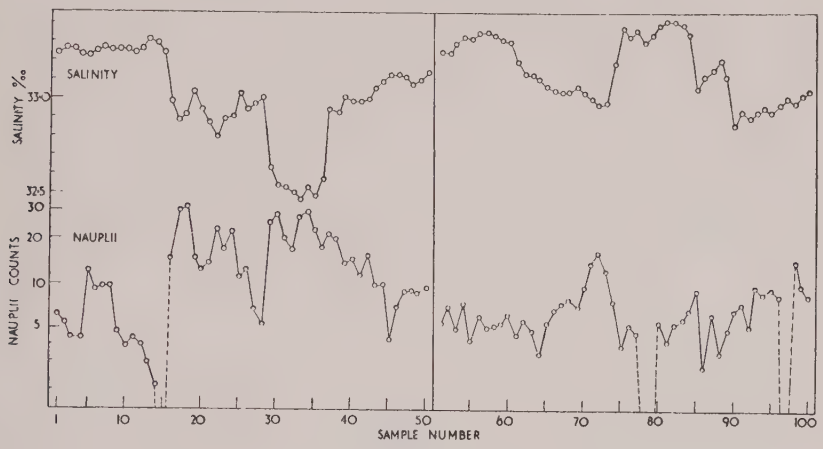


FIG. 4.—Salinity and *Elminius* nauplii. Nauplii numbers adjusted for regression to a constant temperature of 10° C.

The barnacle, *Elminius modestus,* is widely distributed around the shores of Port Nicholson, and has a depth range which permits it to colonize any part of the bottom where conditions are suitable. This species is also known to be tolerant of a considerable proportion of fresh water, and the nauplii are probably capable of surviving at salinities even lower than 16‰, which was the minimum level given by Barnes (1953) for *Balanus balanoides* and *B. crenatus.* Further, it has been shown by Crisp and Davies (1955) that breeding of *E. modestus* can continue at any season provided water temperatures remain above 6° C, but that liberation of embryos from the mantle cavity is stimulated by rising temperature. It seems possible that a lowering of the salinity would assist the rupture of the egg membranes by osmotic pressure, even though the principal agency in hatching appears to be the mechanical efforts of the embryo (Barnes, 1955).

On the above evidence, it seems likely that *Elminius* would be in a spawning condition in most parts of the harbour, but that the actual

release of nauplii at any one time would be in direct proportion to temperature and in reverse proportion to salinity. Owing to the swirling pattern of tidal circulation, most parcels of harbour water will have been in recent contact with *Elminius* beds, and will have had more or less equal chances of becoming populated by nauplii, so that the numbers of relatively short-lived larvae will be dependent more on the present physical properties of the water than on its past history. This is in marked contrast to *Paracalanus*, where past history of the water in the zone is the dominant factor in determining population density, and $T$ and $S$ are only secondary pattern-forming agents.

As a supplementary hypothesis, it might also be postulated that $T$ and $S$ influence the survival of nauplii. It is unlikely, however, that the weakly-swimming nauplii actively seek out those portions of the harbour (as opposed to their own parcel of water) which are best suited to their needs.

### *Podon*

Comparing the two analyses of variance (Tables 3 and 7), it will be seen that elimination of variance due to regressions produces little change. In both cases, the "between zones" mean square is about 3·4, and $F$ is highly significant. Further discussion of the *Podon*:$T$-$S$ relationship will be deferred until the next section, where it will be considered in conjunction with interspecific correlations.

## Interspecific Correlations

In addition to the relationships discussed in the previous section, it is frequently found that the sample counts of various organisms are themselves correlated one to the other. The interpretation of such correlations will be greatly dependent on supplementary biological information regarding the behaviour pattern of the organisms concerned. Thus, if species A and B are correlated, there is nothing in the numerical data to indicate whether A is influencing B, or *vice versa*, or whether both are reacting independently to some external factor. One of the few examples in the literature is given by Tonolli (1958), who notes consistently high positive correlations between two large species of Cladocera and the total of remaining smaller species. He suggests that this is a predator-prey relationship.

In the three species dealt with here, there are significant positive partial correlations between nauplii and *Podon*, naupli and *Paracalanus*, but not between *Podon* and *Paracalanus*. The appropriate regression equations are:

$$\hat{C} = 184 + 1{\cdot}75\ N \qquad \ldots\ldots (6)$$

$$\hat{P} = 11{\cdot}3 + 0{\cdot}79\ N \qquad \ldots\ldots (7)$$

$$\hat{N} = 1{\cdot}84 + 0{\cdot}037\ C + 0{\cdot}20\ P \qquad \ldots\ldots (8)$$

Since the populations of the main sections have been shown to be significantly different, a similar correlation analysis was made within sections. The result was a general reduction of correlations below significance level, except that nauplii:*Podon* (independent of *Paracalanus*) remains probably significant ($r_{NP.C} = 0{\cdot}26^*$). It would appear, then, that interspecific correlation is predominantly a common reaction to some external factor which varies between zones, rather than a direct biological interaction between the species themselves. (The residual, within zones, correlation between nauplii and *Podon* will be discussed further below.) This conclusion is supported by the rather similar size of the three species, which precludes the probability of any predator-prey relationship.

At this point, it is opportune to consider the interaction between temperature-salinity and interspecific correlations. Table 8 gives in the first column the partial interspecific and the total *T-S* correlations for the three species, and in the second column the corresponding partial correlations taking both types of effect into account.*

TABLE 8.—Partial Correlations, Interspecific and *T-S*.

| | Separate effects | Combined effects |
|---|---|---|
| Interspecific correlations ..... | $r_{NP.C} = 0{\cdot}41^{***}$ | $r_{NP.CTS} = 0{\cdot}31^{**}$ |
| | $r_{CN.P} = 0{\cdot}28^{**}$ | $r_{CN.PTS} = 0{\cdot}34^{**}$ |
| | $r_{CP.N} = 0{\cdot}12$ | $r_{CP.NTS} = -0{\cdot}09$ |
| *T-S* correlation ..... ..... | $R_{CTS} = -0{\cdot}07$ | $R_{CTS.PN} = -0{\cdot}22^*$ |
| | $R_{PTS} = 0{\cdot}30^{**}$ | $R_{PTS.CN} = 0{\cdot}11$ |
| | $R_{NTS} = 0{\cdot}50^{***}$ | $R_{NTS.CP} = 0{\cdot}47^{***}$ |

None of the interspecific correlations is greatly altered in its significance level, although the apparent dependence between *Podon* and nauplii is reduced to about half ($0{\cdot}31^2/0{\cdot}41^2 = 0{\cdot}57$) its former value (indicating that temperature and salinity are two of the common factors contributing to this particular interspecific correlation). Nauplii retain about the same *T-S* correlation, and the partial regression coefficients on temperature and salinity are virtually unchanged from equation 5, but both *Podon* and *Paracalanus* show substantial changes. *Podon*:*T-S* is now virtually eliminated, while *Paracalanus*:*T-S* is raised to significance ($R_{CTS.PN} = -0{\cdot}22^*$). The negative sign is attached to the multiple correlation coefficients $R_{CTS}$, $R_{CTS.PN}$ to indicate that the two

*Strictly, the partial correlation coefficients in the second column are not the best mean square estimates owing to the log. transformation of species counts in the *T-S* analysis. Parameter estimates from equations of the form $\log Y = a + bX$ will not be exactly the same as from $Y = Ae^{bX}$, which would be necessary for compatability with the interspecific regression $Y = a + bX$. However, the log. form reduces considerably the labour of computation and is a sufficient approximation for present purposes.

partial correlations are opposite in sign to those for *Podon* and nauplii.

Thus, it appears that the *Podon*:*T-S* correlation is only apparent, and is more probably due to a mutual dependence on some other factor by both *Podon* and nauplii. This is in accordance with the previous observation that there is some residual correlation between these two species after between zones effects have been eliminated. The *Paracalanus*:*T-S* relationship has reappeared, its apparent absence in the pooled data probably being attributable to confusion with interspecific correlations. However, the pooled data *T-S* correlation ($R_{CTS} = 0{\cdot}25^*$) is still slightly higher and is little changed by being made partial on nauplii, so that equation 4 still appears to give the most satisfactory description of the *Paracalanus* distribution.

## Autocorrelations

It is sometimes found that correlations also exist between adjacent sample counts of the same species. Known as autocorrelations, these have been used in ecology as a measure of dispersion, but are unreliable since pronounced over-dispersion may be present without autocorrelation being apparent in the samples. It is possible that correlogram analysis might be used as a measure of the spatial as opposed to the numerical magnitude of aggregation, and thus might supplement the statistic, *c*, previously discussed. (However, the number of samples necessary to obtain information of general significance might be prohibitively large.) Tonolli (1958) records autocorrelation coefficients for two freshwater species in a series of sampling runs with an apparatus combining the features of the Clarke-Bumpus plankton samples and the plankton pump employed here. He notes that the coefficients vary between species and between sets of samples for the same species. Tonolli suggests that these may be attributable both to variations in size of aggregations and to the sampling line intersecting elongated aggregations (*cf. Bainbridge*, 1957) at varying angles. As with interspecific correlations, the interpretation of autocorrelations is very dependent on ancillary data. Thus agregation within one species may be due either to a natural attraction (true contagion) or to a common reaction to external factors.

The autoregression equation for a single species may be expressed in the form:

$$\hat{X}_0 = a + b_1X_1 + b_2X_2$$

where $a$, $b_1$, $b_2$, etc., are constants, $\hat{X}_0$ is the expected number of organisms in a sample, and $X_1$, $X_2$, etc., are the numbers in adjacent samples, 1, 2, etc., spaces removed.

The autoregression coefficients, $b_1$, $b_2$, etc., normally decrease as the degree of proximity, and the analysis is continued for successive values until $b$ no longer differs significantly from zero. The appropriate equations for the three species are as follows:

$$\hat{C}_0 = 62 + 0{\cdot}32\,C_1 + 0{\cdot}38\,C_2 \quad \ldots\ldots (9)$$

$$\hat{P}_0 = 8{\cdot}2 + 0{\cdot}63\,P_1 \quad \ldots\ldots (10)$$

$$\hat{N}_0 = 8{\cdot}5 + 0{\cdot}62\,P_1 \quad \ldots\ldots (11)$$

The first regression coefficient in each case, and in *Paracalanus* the first and second, are highly significant. It would thus appear that the spatial scale of aggregation is somewhat larger in *Paracalanus* than in the other two species. This is consistent with the differences in behaviour already noted, *Paracalanus* aggregation being related more to the individual history of the zones, while nauplii are dependent on the detailed pattern of physical properties. The coefficient of multiple correlation for autoregression (Table 9) is in all cases higher than for any of the other correlations described. However, if the same autocorrelations are computed on a "within zones" basis, some striking differences are found. For *Paracalanus*, $R$ falls from 0·61 to 0·09, suggesting that the apparent "contagion" may be explained entirely by differences in population density between zones. *Podon* and nauplii still retain significance within zones, but $R^2$ is in each case reduced to much less than half of its former value. A further reduction could be made by computing partial regressions on $T$, $S$, and other species, The actual values of these regressions have not been calculated, as the additional labour of computation did not seem warranted, but it is evident that the initial evidence of "contagion" may be partly or wholly accounted for in every case, without resorting to any hypothetical gregarious or "contagious" behaviour of the species concerned.

## The Joint Contribution to Over-dispersion of all Factors Combined

Table 9 summarizes the multiple correlation coefficients appropriate to the relationships discussed above. As has been previously shown, if the residual variance independent of regression may be attributed to chance, $R^2$ will be about 0·9. It will be seen from the table that, although some of the regressions make a substantial contribution to over-dispersion, all fall short of accounting for it completely. Nor can all regressions combined afford a complete explanation. For example, in the nauplii, which provide the most promising case, combining temperature, salinity, and interspecific correlations gives $R^2 = 0{\cdot}36$, while if autocorrelation is also taken into account, $R^2 = 0{\cdot}5$ (approximately). Since this is still appreciably less than 0·9, it must be assumed that other factors are still to be accounted for.

## Conclusions

The more significant conclusions may be summarized in terms, firstly of the three species, and secondly of the different types of relationship.

TABLE 9.—Summary of Correlation and Regression Analysis.

| Species | | *T-S* correlation $R^2$ | *T-S* correlation $R$ | d.f. | Interspecific correlation $R^2$ | Interspecific correlation $R$ | d.f. | Autocorrelation $R^2$ | Autocorrelation $R$ | d.f. |
|---|---|---|---|---|---|---|---|---|---|---|
| *Paracalanus parvus* ..... ..... | Pooled | 0·005 | 0·07 | 97 | 0·06 | 0·25* | 98 | 0·37 | 0·61*** | 95 |
| | Within zones | 0·11 | 0·33** | 73 | 0·02 | 0·13 | 82 | 0·009 | 0·09 | 55 |
| *Podon polyphemoides* ..... | Pooled | 0·09 | 0·30** | 97 | 0·15 | 0·39*** | 98 | 0·40 | 0·63*** | 96 |
| | Within zones | 0·02 | 0·15 | 73 | 0·02 | 0·14 | 82 | 0·10 | 0·32** | 64 |
| *Elminius modestus* nauplii ..... | Pooled | 0·25 | 0·50*** | 97 | 0·22 | 0·47*** | 97 | 0·38 | 0·62*** | 96 |
| | Within zones | 0·07 | 0·27* | 73 | 0·11 | 0·26* | 82 | 0·16 | 0·40*** | 64 |

*Paracalanus parvus* is an oceanic species, probably introduced to the harbour by tidal action. The harbour population may be regarded as a series of sub-populations, each occupying a zone of water which is relatively homogeneous and distinguishable from other zones by its physical properties. The numerical abundance of each sub-population is dependent more on the past history of the zone than on any properties of water at the time of observation. Within each zone, individuals show a preference for salinities nearer to those of the ocean (i.e., higher). A slight negative correlation to temperature exists, but may be due to chance. There is no evidence of true contagion (gregarious behaviour) in *Paracalanus*, any aggregation being attributable, at least on the present sampling scale, to the differing populations between water zones.

*Podon polyphemoides* has a pattern of distribution which appears to be unrelated to temperature or salinity, but has a small though significant correlation with *Elminius nauplii*, which may be due either to mutual attraction or to some common environmental preference. Some apparent contagion remains after elimination of other factors, but it seems more probable that aggregation is due to external causes.

The stage VI nauplii of *Elminius modestus* are strongly correlated with higher temperature and lower salinity, suggesting that these two water characteristics are (within the range encountered in these samples) most favourable for the liberation of larvae by the parents. There is a correlation with *Podon* and with *Paracalanus*, although, owing to the similar sizes of the three species, a predator-prey relationship seems unlikely. If either *Podon* or *Paracalanus* fed on the smaller, newly hatched nauplii, it would be expected that the correlation would be negative. As with *Podon*, there is apparent contagion, all or nearly all of which may be accounted for by external causes.

Four different categories of pattern-determining factor may be distinguished, and their significance discussed, particularly as regards oceanic plankton:

(1) Water discontinuities.
(2) Water inhomogeneities.
(3) Interspecific relationships.
(4) Intraspecific relationships.

Water discontinuities are likely to be of a dynamic nature, the pattern seen here being in some respect analagous—though on a smaller scale—to oceanic convergences, and the boundaries of ocean currents, where conflicting water movements continue to renew differences, both in physical properties and plankton populations. Apart from certain restricted regions, aggregations of this type are unlikely to be of general occurrence in the open ocean.

Water inhomogeneities in the ocean are usually assumed to be of smaller magnitude than those of inshore waters. The "within zones" mean standard deviations of $T$ and $S$ in the present samples are 0·06° C

and 0·05‰ respectively. Thus, within any one zone, 95% of the observations will fall within a range of 0·24° C and 0·20‰.

Liebermann (1951) has demonstrated that spatial temperature fluctuations with mean amplitude of about 0·1° C (i.e., a total range of 0·2° C) within a distance of 60 cm are of common if not of universal occurrence in depths up to 60 metres (200 ft) in the open sea. This is of similar magnitude to the temperature fluctuations which are influencing the within zones behaviour of *Paracanalus*.

References to equation 4 shows that a fall in numbers of 17% will accompany a 0·1° C change and 31% for 0·2 ° C. Although the matter requires further investigation, it seems not unreasonable to suspect that a copepod in the ocean might swim a distance of up to 60 cm horizontally, or alternatively control its vertical migration within the same limits in order to obtain a slightly preferable micro-climate. It would be interesting to determine whether salinity fluctuations in the ocean are also of similar magnitude to those quoted for the harbour, particularly since salinity would appear on present evidence to be a rather more potent factor than temperature, an observation which is also supported by the findings of Barnes and Marshall (1951).

Interspecific relationships (other than those induced by inhomogeneity) would be just as likely to occur in any part of the ocean, regardless of its physical structure. Other data at present in preparation have indicated that appreciably higher correlations than those shown here may at times be found, and that they may be either positive or negative in sign. It is possible that in the present case the correlations have been masked owing to the fact that only a relatively small number of species have been counted; and thus insufficient of the interacting factors have been isolated.

Intraspecific correlations (or autocorrelations), although appearing highly significant in the initial analysis, have, in fact, proved to be wholly or partly attributable to other factors. There is little doubt that some organisms do on occasion form gregarious aggretions (as in schooling fish), but the present information emphasizes the need for caution, in that neither over-dispersion nor autocorrelation are in themselves conclusive evidence of contagion in the sense defined in the introduction. On the other hand, the absence of autocorrelation from a set of samples does not necessarily imply that contagion is absent. Thus, in the present series, it is quite possible that further and more persistent autocorrelation would have been revealed if the sample spacing had been appreciably reduced.

In conclusion, it must be emphasized that the interpretation of correlation data alone must always involve some measure of speculation. Unless all causal agencies have been accounted for, weaker though still significant correlations will tend to be obscured or even reversed in sign. While there is little doubt of the reality of the relationship where higher statistical significance is found, the actual sequence of cause and effect cannot be finally revealed without supplementary biological evidence of behaviour patterns.

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## REFERENCES

BAINBRIDGE, R., 1957: The Size, Shape, and Density of Marine Phytoplankton Concentrations. *Biol. Rev. 32*: 91–115.

BARNES, H., 1952: The Use of Transformations in Marine Biological Statistics. *J. Cons. int. Explor. Mer. 18*: 61–71.

————, 1953: The Effect of Lowered Salinity on Some Barnacle Nauplii. *J. Anim. Ecol. 22*: 328–30.

————, 1955: The Hatching Process in Some Barnacles. *Oikos 6*: 114–23.

BARNES, H.; MARSHALL, S. M., 1951: On the Variability of Replicate Plankton Samples and Some Applications of "Contagious" Series to the Statistical Distribution of Catches Over Restricted Periods. *J. Mar. biol. Ass. U.K. 30*: 233–63.

BARY, B. M., 1959: Species of Zooplankton as a Means of Identifying Surface Waters and Demonstrating their Movements and Mixing. *Pacif. Sci. 13*: 14–54.

BRODIE, J. W., 1958: A Note on Tidal Circulation in Port Nicholson, New Zealand. *N.Z. J. Geol. Geophys. 1*: 684–702.

CASSIE, R. M., 1957: The Sampling Problem, with Particular Reference to Marines Organisms. *Proc. N.Z. ecol. Soc. 4*: 37–9.

————, 1958: Apparatus for Investigating Spatial Distribution of Plankton. *N.Z. J. Sci. 1*: 436–48.

CRISP, D. J.; DAVIES, P. A., 1955: Observations *in Vivo* on the Breeding of *Elminius modestus* Grown on Glass Slides. *J. Mar. biol. Ass. U.K., 34*: 357–80.

KNIGHT-JONES, E. W.; WAUGH, G. D., 1949: On the Larval Development of *Elminius modestus* Darwin. *J. Mar. biol. Ass. U.K. 28*: 413–28.

KRAMER, A., 1894: On the Most Frequent Pelagic Copepods and Cladoceres of the Hauraki Gulf. *Trans. N.Z. Inst. 27*: 214–23.

LIEBERMANN, L., 1951: Effect of Temperature Inhomogeneities in the Ocean on Propagation of Sound. *J. acoust. Soc. Amer. 23*: 563–70.

REED, D. G.; STEWART, T., 1949: A Streamline Cable Depressor. *J. Mar. Res. 8*: 226–36.

TONOLLI, V., 1958: Ricerche sulla Microstruttura di Distribuzions dello Zooplankton nel Lago Maggiore. *Mem. Inst. ital. Idrobiol. de Marchi 10*: 125–52.

## APPENDIX

### MATHEMATICAL MODELS FOR ANALYSIS OF VARIANCE AND COVARIANCE

The following is a statement of the mathematical models used, and the null hypotheses tested, in the analyses of variance (Tables 3, 5, and 6).

*Table 3*:

Model: $X_{ij} = m + \epsilon_j + \epsilon_{ij}$
Null hypothesis $\epsilon_j = 0$ rejected

where $X_{ij}$ = log numbers of individuals in $i$ th sample of the $j$ th zone
$m$ = population mean of all values of $X$
$\epsilon_j$ = deviation of mean of $j$ th zone from population mean
$\epsilon_{ij}$ = deviation of $i$ th sample from mean of $j$ th zone

*Table 5*:

Model: $X_{ij} = m + (\beta + \epsilon\beta_j)\Delta S_{ij} + \epsilon_j + \epsilon_{ij}$
Null hypothesis: 1. $\epsilon_j = 0$ rejected

2. $\epsilon_j = 0$ accepted
where $X_{ij}$, $m$ = as above
$\Delta S_{ij}$ = deviation from mean salinity in $i$ th sample of $j$ th zone
$\beta$ = population regression coefficient of $X$ on salinity
$\epsilon\beta_j$ = deviation of regression on salinity in $j$ th zone from population regression
$\epsilon_j$ = deviation, independent of regression, of mean of $j$ th zone from population mean
$\epsilon_{ij}$ = deviation of $i$ th sample from mean of $j$ th zone, both independent of regression

*Table 6*

Model: $X_{ij} = m + (\beta + \epsilon\beta_j)\Delta S_{ij} + (\gamma + \epsilon\gamma_j)\ \Delta T_{ij} + \epsilon_j + \epsilon_j + \epsilon_{ij}$

Null hypothesis
1. $\epsilon_j = 0$ rejected
2. $\epsilon\beta_j + \epsilon\gamma_j = 0$ accepted

where $X_{ij}$, $m$, $\Delta S_{ij}$, $\epsilon_j$, $\epsilon_{ij}$ = as above
$T_{ij}$ = deviation from mean salinity in $i$ th sample of $j$ th zone
$\beta$, $\epsilon\beta_j$ = as above, but for partial regression on salinity, independent of temperature
$\gamma$ = population partial regression coefficient of $X$ on temperature independent of salinity.

$\epsilon\gamma_j$ = deviation from partial regression on temperature in $j$th zone, from population regression

*Table 7*

Model: $X_{ij} = m + \beta\Delta S_{ij} + \gamma\Delta T_{ij} + \epsilon_j + \epsilon_{ij}$

Null hypothesis: $\epsilon_j = 0$ rejected for both species

All symbols as for Table 6.

# NEW ZEALAND TALL OIL: ISOLATION AND IDENTIFICATION OF HIGH MOLECULAR WEIGHT *NORMAL* SATURATED FATTY ACID CONSTITUENTS

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## *Summary*

Trace amounts of pure *n*-octadecanoic, *n*-eicosanoic, *n*-docosanoic, and *n*-tetracosanoic acids have been isolated from New Zealand tall oil.


## Introduction

Earlier investigations on a sample of New Zealand tall oil (sample J/23) showed it to contain minor proportions (3·5 to 4%) of saturated fatty acids, the main components being rosin acids (approx. 50%), $C_{18}$ unsaturated fatty acids both conjugated and unconjugated (approx. 39·5%), and unsaponifiable matter (approx. 7%). Of the saturated fatty acids, *n*-hexadecanoic (palmitic) acid and the $C_{17}$ branched-chain acid (+)-14-methylhexadecanoic acid, where isolated and identified (Hansen & Cooke, 1957). *n*-Hexadecanoic acid was found to be present to the extent of about 3·1% of the weight of the tall oil, while (+)-14-methylhexadecanoic acid occurred in trace amounts only (approx. 0·16%).

In the work reported in this present publication, which is part of a project to determine the nature and composition of New Zealand tall oil, with particular reference to the fatty acids, the following *normal* saturated fatty acids have been isolated in trace amounts and conclusively identified: *n*-octadecanoic (stearic) acid, *n*-eicosanoic (arachidic) acid, *n*-docosanoic (behenic) acid, and *n*-tetracosanoic (lignoceric) acid.

The techniques employed in the separation and purification of these fatty acid constituents were fractional distillation *in vacuo* of the methyl esters, and repeated low temperature crystallization from solvents.

## Experimental

The sample of tall oil used in this work (K/179) was prepared from "black liquor skimmings" produced during the manufacture of paper pulp by the sulphate process from New Zealand grown *Pinus radiata*. The "black liquor skimmings" were acidified with sulphuric acid and the resulting tall oil was extracted with light petroleum (b.p. 40° to 60°) and repeatedly washed with water.

As a means of separating fatty acids from rosin acids, the total tall oil acids (1029·5 g) were treated with methyl alcohol containing 5% (w/v) concentrated sulphuric acid in order to esterify the fatty acids, and the rosin acids were washed out with 5% sodium hydroxide, in accordance with the method followed by Anderson & Wheeler (1945). Of the 430·0 g methyl esters produced, 405·0 g were fractionally distilled in a 122 × 3·2 cm column (column B, Shorland, 1952) fitted with a coiled nichrome spiral. Fractionation yielded twenty-one fractions (K/179, 2, L1 to L21) and a residue. The high molecular weight components reported in this paper were then isolated by distillation *in vacuo* of fractions freed of unsaponifiable matter, followed by low temperature crystallization. Identification of component acids was established by chemical and physical constants, including saponification equivalents, melting points, mixed melting points with pure substances, combustion analyses, iodine values, and X-ray measurements.

Melting points were determined in closed capillaries and are uncorrected. X-ray measurements were made with a Philips Geiger X-ray spectrometer in which manganese-filtered iron K$\alpha$ radiation was used. In the preparation of samples for X-ray analysis, samples were melted on a glass slide and cooled.

### *n*-Octadecanoic (stearic) acid

Fraction D21S6S (wt. 1·10 g). M.p. 69·7° to 70·3° (reported values, 69·6°*, 69·7°†); when mixed with an equal quantity of pure *n*-octadecanoic acid (m.p. 69·6° to 69·8°) gave m.p. 69·2° to 69·7°; sap. equiv. 284·5 (calc. for $C_{18}H_{36}O_2$, 284·5); combustion analysis‡, C 76·3% H 12·9% (calc. for $C_{18}H_{36}O_2$, C 76·0% H 12·8%); iodine value 1·2; X-ray long spacing 39·95 Å (reported values 40·0 Å†, 39·75 Å*); $n_D^{80}$ 1·4297 (reported (Dorinson, McCorkle, & Ralston, 1942) $n_D^{80}$ 1·4299). Methyl ester: m.p. 37·9° to 38·5° (reported m.p. 38·7°*); when mixed with pure methyl octadecanoate (m.p. 38·2° to 38·8°) gave m.p. 38·3° to 39·2°.

Fraction D16S5S (wt. 0·69 g). M.p. 68·8° to 69·4°; when mixed with an equal quantity of pure *n*-octadecanoic acid (m.p. 69·7° to 69·8°) gave m.p. 69·2° to 69·7°; sap. equiv. 284·3; combustion analysis‡, C 75·7% H 12·6%; iodine value 1·2; X-ray long spacing 40·3 Å (a sample of pure *n*-octadecanoic acid measured at the same time gave a value of 39·9 Å). Methyl ester: m.p. 37·2° to 38·1°.

Content of *n*-octadecanoic acid in tall oil sample: approximately 0·2% by weight.

### *n*-Eicosanoic (arachidic) acid

Fraction D13SS (wt. 0·59 g). M.p. 75·7° to 76·2° (reported values 75·35°*, 75·1°†); when mixed in equal proportions with pure *n*-eicosanoic acid from butterfat (m.p. 74·8° to 75·3°) gave m.p. 75·4° to 76·3°; sap. equiv. 312·3 (calc. for $C_{20}H_{40}O_2$, 312·5); combustion analysis‡, C 77·0% H 12·8% (calc. for $C_{20}H_{40}O_2$, C 76·8% H 12·9%); iodine value 0·4; X-ray long spacing 44·0 Å (reported

value 44·15 Å*, 43·9 Å†). Methyl ester: m.p. 45·3° to 46·2° (reported m.p. 46·6°*).

Content of *n*-eicosanoic acid in tall oil sample: approximately 0·06% by weight.

### *n*-Docosanoic (behenic) acid

Fraction D7S3S (wt. 1·32 g). M.p. 79·5° to 80·0° (reported values, 79·95°*, 79·9°†); when mixed with an equal quantity of *n*-docosanoic acid from ox fat (m.p. 78·9° to 79·6°) gave m.p. 79·3° to 79·5°; sap. equiv. 342·0 (calc. for $C_{22}H_{44}O_2$, 340·6); combustion analysis‡, C 77·3% H 13·0% (calc. for $C_{22}H_{44}O_2$, C 77·6% H 13·0%); iodine value 0·3; X-ray long spacing 48·8 Å (reported values 48·3 Å*†). Methyl ester: m.p. 52·0° to 53·1° (reported m.p. 53·3°*).

Fraction D8S6S (wt. 0·19 g). M.p. 79·2° to 79·4°; when mixed with an equal quantity of *n*-docosanoic acid (m.p. 78·9° to 79·6°) gave m.p. 79·1° to 79·4°.

Content of *n*-docosanoic acid in tall oil sample: approximately 0·16% by weight.

### *n*-Tetracosanoic (lignoceric) acid

Fraction D6(b)S11S (wt. 0·38 g). M.p. 83·7° to 84·2° (reported values, 84·15°*, 83·9°†); when mixed with an equal quantity of *n*-tetracosanoic acid from butterfat (m.p. 84·1° to 84·3°) gave m.p. 83·6° to 84·3°; sap. equiv. 365·0 (calc. for $C_{24}H_{48}O_2$, 368·6); combustion analysis, C 78·2% H 13·1% (calc. for $C_{24}H_{48}O_2$: C 78·2% H 13·1%); iodine value 0·0; X-ray long spacing 52·4 Å (reported value 52·6 Å*, 52·9 Å†). Methyl ester: m.p. 57·2° to 58·0° (reported m.p. 57·8°*).

Content of *n*-tetracosanoic acid in tall oil sample: approximately 0·05% by weight.

## Discussion

In the present investigation of New Zealand tall oil, trace amounts of *n*-octadecanoic (stearic), *n*-eicosanoic (arachidic), *n*-docosanoic (behenic), and *n*-tetracosanoic (lignoceric) acids have been isolated in the pure state and identified by their chemical and physical constants. *n*-Hexadecanoic (palmitic) acid was earlier isolated (Hansen & Cooke, 1957).

The presence in American tall oil of *n*-hexadecanoic, *n*-octadecenoic and higher saturated fatty acids has been reported by Herrlinger (1954), but the components higher than *n*-octadecanoic acid were not specified in this paper. A sample of Japanese tall oil is reported to contain *n*-

*Francis & Piper, 1939.
†Stenhagen & von Sydow, 1953.
‡Combustion analysis by Dr A. D. Campbell, Organic Microanalytical Laboratory, Chemistry Department, University of Otago, New Zealand.

hexadecanoic, *n*-octadecanoic, and *n*-tetracosanoic acids (Matsumoto & Hirai, 1954). Sandquist, Gorton & Bengtsson (1931) report having isolated *n*-tetracosanoic acid from Swedish tall oil, but they make no reference to other high molecular weight saturated acids being present. Bergström (1957), however, reports that Swedish tall oil contains all the *normal* even-numbered saturated fatty acids from $C_{12}$ to $C_{24}$ inclusive. Investigations on another wood product, namely Swedish "pitch wood" by Bergström, Ryhage, & Stenhagen (1956) have revealed that so-called "carnauba acid" from this source is a mixture of 72-76 mol.% *n*-docosanoic acid and 24-28 mol.% *n*-tetracosanoic acid, together with a trace of *n*-eicosanoic acid. It was further established by monolayer and mass spectrometric techniques employed in their work, that there was no evidence for acids higher than *n*-tetracosanoic in "carnauba acid". In this present work also, acids of higher molecular weight than that of *n*-tetracosanoic acid were not isolated.

By means of paper chromatographic analyses, Perilä (1956) has detected in the Finnish hardwoods aspen and birch both the odd and even-numbered *n*-saturated fatty acids from formic to octanoic together with the remaining even-numbered members of the series up to *n*-hexacosanoic acid. The fatty acid composition of the lipid extract of *Pinus radiata* has not been determined, but in the present analysis of tall oil produced from this species of pine, *n*-odd numbered fatty acids have not been found.

The high molecular weight saturated components in the sample of tall oil analysed (K/179) were found to be present in trace quantities only. Based on the weights of the fractions isolated, *n*-$C_{18}$ constitutes approximately 0·2% of the total weight of the tall oil sample, while the contents of the *n*-$C_{20}$, *n*-$C_{22}$, and *n*-$C_{24}$ components approximate 0·06%, 0·16%, and 0·05% respectively. The content of *n*-hexadecanoic acid in this investigation represents about 2·5% of the weight of the tall oil. A former sample of New Zealand tall oil (J/23, Hansen & Cooke, 1957) was found to contain approximately 3·1% of this acid. Variations in composition will occur, however, because of the difficulty in obtaining representative samples of skimmings.

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## REFERENCES

ANDERSON, R. H.; WHEELER, D. H., 1945: *Oil & Soap, 22* : 137-41.

BERGSTROM, H., 1957: "Wood Chemistry Research at Kolningslaboratoriet", p. 11. Ivar Haeggström Boktryckeri AB, Stockholm.

BERGSTROM, H.; RYHAGE, R.; STENHAGEN, E., 1956: *Svensk Papp. Tidn. 59* : 593-98.

DORINSON, A.; MCKORKLE, M. R.; RALSTON, A. W., 1942: *J. Amer. chem. Soc. 64* : 2739.

FRANCIS, F.; PIPER, S. H., 1939: *J. Amer. chem. Soc. 61* : 577-81.

HANSEN, R. P.; COOKE, N. J., 1957: *J. Sci. Fd. Agric., 8* : 331-33.

HERRLINGER, R., 1954: *J. Amer. Oil Chem. Soc. 31* : 508-12.

MATSUMOTO, T.; HIRAI, C., 1954: *J. oil Chem. Soc. (Japan) 3* : 270. *Chem. Abstr.* 1955 : *49* : 9272.

PERILA, O., 1956: Saturated Fatty Acids of Stem Cells of Birch (*Betula verrucosa*) and Aspen (*Populus tremula*). *Ann. Acad. Sci. fenn. Ser.* A. II. Chemica.

SANDQUIST, H.; GORTON, J.; BENGTSSON, E., 1931: *Ber. chem. Gesselschaft 64* : 2172.

SHORLAND, F. B., 1952: *J. appl. Chem. 2* : 438-40.

STENHAGEN, E.; VON SYDOW, E., 1953: *Arkiv. Kemi Bd. 6*, Nr. 29 : 309.

# THE TOXICITY OF MUSCLE, LIVER, AND HEART OF DEER POISONED WITH SODIUM MONOFLUOROACETATE (1080)

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***Summary***

Meat, hearts, and livers from eight deer poisoned with 1080 in a field experiment have been examined for poison content and assessments made of the potential toxicity of these tissues for man. The most toxic meat produced contained 0·92 mg of 1080 per 100 g. It is concluded that acute poisoning in a man eating these tissues from a deer poisoned with 1080 and shot before symptoms of poisoning appeared could not occur, and that chronic poisoning from daily ingestion of the tissues would be most unlikely.

## Introduction

The successful use of sodium monofluoroacetate (1080) as a rabbit poison in New Zealand and Australia has given hope that it may be a valuable weapon for destroying deer in areas where their numbers have reached pest proportions. The New Zealand Forest Service is investigating this possibility. Secondary poisoning in animals eating the carcasses of other animals poisoned with 1080 is well known, members of the Canidae being especially susceptible. As there is always a time lag between the ingestion of 1080 and the onset of symptoms, it has been necessary, on public health grounds, to determine whether there could be any possibility of acute poisoning in humans who might eat the meat of deer which had ingested 1080 and been shot before showing symptoms of poisoning. Hagan *et al.* (1950) give the levels of 1080 in the tissues of rats poisoned with different levels of 1080, but in the literature available no data on the toxicity of the meat of ruminants poisoned with 1080 have been found.

Data on the levels of 1080 found in meats, livers, and hearts of deer poisoned with 1080 in a field experiment in the Caples Valley and the toxicity of the meats to dogs are presented, together with assessments of the potential toxicities of the meats to man.

## Experimental

In a trial of which the primary purpose was to assess the efficiency of the poison against fallow deer (*Cervus dama* L.) under field condi-

tions, the deer were pre-fed in their natural habitat with unpoisoned whole and chopped carrot, to accustom them to the bait, and then poisoned with chopped carrot treated with an aqueous solution of 1080 applied at the rate of half a pound of the poison to 800 lb of carrot. The poisoned bait was dropped from the air on 7 November 1958. The primary object of the trial precluded any disturbance of the deer during the poisoning operations and in only one case were samples obtained from an animal killed other than by poisoning. Autopsies were carried out at 24 to 36 hours after death on a number of animals and seven were selected for sampling so that material from animals with a wide range of carrot bait in their rumens would be included. The seven animals selected included one of two red deer (*Cervus elaphus* L.) poisoned incidentally during the operation. Samples of heart, liver, and meat from the muscle group at the posterior aspect of the femur were taken, care being exercized to avoid contamination of the samples with alimentary contents. Samples were also taken from a fallow deer freshly killed. Attempts were made to pick out and weigh the pieces of carrot bait in the rumen of each of the eight deer selected for sampling. Owing to the carrot having become soft and mushy through partial digestion, it was impossible to separate it from the other ruminal contents and visual estimates only of the amounts present could be made. The samples were packed separately in plastic bags and flown to Wallaceville, about one day being occupied in transit. All samples were washed with cold water on arrival and the portions of the samples of meat intended for feeding tests on dogs were stored in separate plastic bags at — 20° C. The livers, hearts, and portions of meat intended for analysis were stored in glass jars in a cold room at 3° C. Preliminary work with healthy mongrel dogs aged from one to three years and weighing between 12·2 and 24·0 kg showed that 0·08 mg of 1080 per kg of body weight given orally killed all seven dogs dosed at this level. The poison was given as a solution pipetted on to ground grain meal in a gelatine capsule which was then folded into a piece of meat. The dogs were fed the poison at their normal once-daily feeding time, a normal meal of raw meat being given after the poison was fed. Time from dosing to death in these dogs varied from nine and a half to fifteen hours approximately. One dog dosed similarly with 0·065 mg 1080 per kg showed no symptoms. The deer-meat samples were thawed out as required and fed in weighed amounts to healthy weighed mongrel dogs aged between one and three years. The meat and the juice obtained in thawing it out was usually taken readily, but in two cases had to be force fed. The supply of dogs available was limited, but earlier work (unpublished) on the toxicity to dogs of meat from sheep poisoned with known doses of 1080 gave some guide as to how much of the meat samples should be fed to dogs of given weights to produce kills or survivals. With the meats of higher toxicity, amounts sufficient to kill were fed, but with those of lower toxicity the amounts necessary to kill were not determined. Some dogs showing no effects from a feeding were used again, at least thirteen days being allowed before a new test feeding. At the end of the trials, three surviving dogs in this category were tested for the development of tolerance to 1080 by dosing them

with the poison at the normal certain fatal dose rate, i.e., 0·08 mg/kg. Two of the dogs died and the third was very severely affected and was slaughtered in extremis. It was concluded that no tolerance to 1080 had developed and that the re-use of dogs would not vitiate the results. The samples of hearts and livers were not large enough to allow feeding tests on dogs with graded amounts to be carried out. All dogs were examined ante- and post-mortem to verify that they were free from disease .

### *Analytical*

Organic fluorine in the tissues was determined by the method of Ramsey and Clifford (1949) digestion with pancreatin being used. In the final titration with thorium nitrate, direct titration was used instead of the bleaching titration with standard sodium fluoride. The method gave approximately 80% recoveries of monofluoroacetate added to normal tissues.

## Results

Table 1 sets out the results of the feeding trials to dogs on the eight samples of meat. The estimated amounts of poisoned carrot in the

Table 1.—Feeding of Venison from 1080 Poisoned Deer to Dogs.

| Deer | Bait in Rumen, Estimated at Autopsy | Dog Wt. (kg) | Weight Meat Fed (g) | Result | 1080 Content of Meat. (mg/100 g) (From dog feeding trial) |
|---|---|---|---|---|---|
| A | Few grammes | 14·2 | 531 | No effect | $< 0·214$ |
| B | Few grammes | 9·5 | 357·5 | No effect | $< 0·213$ |
| C | 30 grammes | 24·4 | 457·5 | No effect | |
| | | 15·0 | 436 | No effect | |
| | | 15·0 | 595 | No effect | $< 0·202$ |
| D | 900 grammes | 14·1 | 70 | No effect | |
| | | 14·4 | 142·5 | No effect | |
| | | 14·5 | 287 | No effect | $< 0·404$ |
| E | 1000 grammes | 13·8 | 68·5 | No effect | |
| | | 17·9 | 133 | No effect | |
| | | 15·6 | 155·8 | Died | |
| | | 16·3 | 161·5 | Died | $< 1·08 > 0·81$ |
| F | 1800 grammes | 13·7 | 68·3 | No effect | |
| | | 19·4 | 144 | Died | |
| | | 14·2 | 140·2 | Died | $< 1·08 > 0·81$ |
| G | 2000 grammes | 20·7 | 102·7 | No effect | |
| | | 24·0 | 178 | No effect | |
| | | 20·4 | 202 | Died | $< 1·08 > 0·81$ |
| H* | 1350 grammes | 17·4 | 86·4 | No effect | |
| | | 17·9 | 177 | No effect | |
| | | 14·1 | 278 | No effect | $< 0·406$ |

*Red deer 135-165 kg in weight } Estimated.
Others, Fallow deer 45-55 kg in weight }

rumens of the eight deer samples are shown and also the amounts of 1080 in the meats assessed from the feeding trials.

Table 2 shows the amounts of 1080 recovered by chemical analysis from the meats, hearts, and livers of the eight deer.

TABLE 2.—1080 Concentrations in Tissues (mg/100 g wet weight)

| Deer | Meat | Heart | Liver |
|---|---|---|---|
| A | 0·150 | 0·047 | 0·092 |
| B | 0·116 | 0·109 | 0·075 |
| C | 0·114 | 0·085 | 0·149 |
| D | 0·316 | 0·340 | 0·160 |
| E | 0·653 | 0·358 | 0·216 |
| F | 0·737 | 0·75 | 0·39 |
| G | 0·686 | 0·812 | 0·405 |
| H | 0·303 | 0·255 | 0·094 |

*Assessment of Effects of Meat on Man*

Any assessment of the probable effects of the meats on man is dependent on information available on the effects of known amounts of 1080 on man. Some information is given by Peters (1953) who states that Lord Adrian, in two auto-experiments, took without harm doses equivalent to 0·4 and 0·65 mg/kg of body weight. Various estimates of the acute fatal dose for man have been made, and McGirr and Papworth (1955) quote an estimated L.D. 50 figure of 2·5 mg/kg attributed to U.S. Public Health Service. In the assessments which follow in Table 3 a figure of 2·0 mg/kg as the probable fatal dose for man has been used.

The assessments are based on the results of the feeding trials on dogs and on the chemical analysis of the meats. The amounts of 1080

TABLE 3.—Toxicity of Meat to Man.

| Deer | Expected Effect on 68-kg Man. (From dog-feeding trials) | Amount of Meat to Kill 68-kg Man. (From adjusted analytical data) |
|---|---|---|
| A | 64 kg meat would not harm | 72 kg |
| B | 64 kg meat would not harm | 94 kg |
| C | 67 kg meat would not harm | 95 kg |
| D | 33·7 kg meat would not harm | 34 kg |
| E | 12·6 kg meat would not harm | |
| | 16·8 kg meat would kill | 16·7 kg |
| F | 12·6 kg meat would not harm | |
| | 16·8 kg meat would kill | 14·8 kg |
| G | 12·6 kg meat would not harm | |
| | 16·8 kg meat would kill | 15·9 kg |
| H | 33·5 kg meat would not harm | 36 kg |

determined by chemical analysis have been adjusted by multiplying by 100/80 to compensate for the known loss in analysis.

## Discussion

The dog is a good test animal for 1080, since it is highly sensitive to the poison and the margin between a non-lethal and a lethal dose for the dog is small. The biological tests on these animals have given an overall picture of the toxicity of the meats and give a more complete picture than results based on chemical analysis for organic fluorides alone. It could be argued that in the latter case no chemical distinction was made between fluoroacetate and fluorocitrate. Of the possible influence of this latter substance a statement by Peters (1953) is important. He states, *inter alia*, that "injection of the inhibitor" (fluorocitrate) "has not killed animals so far, which we interpret to mean that it does not penetrate to the active centres". From this it follows that it would be most improbable that fluorocitrate present in the meat and taken by mouth could contribute to the toxicity of the meat. Peters (1953) points out the very small amounts of fluorocitrate that are formed in tissues of animals poisoned with fluoroacetate, and hence for practical purposes the organic fluoride found by chemical analysis could all be regarded as being present as fluoroacetate. The agreement between the biological and the chemical methods in assessing the probable toxicities of the meats to man would support these conclusions.

Deer A was the only animal killed other than by poisoning and this animal was obviously affected by the poison when it was run down and killed. It would be the kind of poisoned animal most likely to be shot and taken for meat. Data of Bissell and Brunetti quoted by Rudd and Genelly (1956) indicate that the lethal dose of 1080 for deer is similar to that for sheep, i.e., about 0·45 mg/kg of body weight. With the exception of Deer H, which was approximately three times as heavy as the others, the deer were estimated to weigh between 45 and 55 kg and would have required between 20 and 25 mg of 1080 to kill them. These amounts of poison would have been contained in 32 to 40 g of bait if the poison had been applied uniformly to the carrot. From the very small amounts of carrot in Deer A and B at autopsy it is concluded either that the carrot had been partly digested or that the distribution of poison in the bait had not been uniform. It is estimated that Deer G had ingested over 50 lethal doses of 1080 and, from earlier dosing work with sheep, had probably died within two or three hours from starting to ingest the poisoned bait. On a similar estimate Deer D would have ingested over 20 lethal doses and would have died within four hours. Even the large red Deer H had probably eaten about ten lethal doses and would have died in very little longer time. These short survival times would not provide much opportunity for such deer to be shot and used for meat. In the whole poisoning trial, in which a large number of deer were poisoned, no dead animal was found at a distance greater than three hundred yards from the area on which the

baits were laid. Deer with a low bait intake such as A, B, and C could possibly live for up to thirty hours, if the poison ingested were about one lethal dose. This would give them ample time to move out of the poisoning area if they so desired, or were disturbed. The toxicities of the meats of such animals have been shown to be so low that acute poisoning could not occur in a man eating these meats. It is obvious that the meat from a deer ingesting a sub-lethal dose of 1080 would be even less toxic than any of the meats examined in this work. It is highly probable from the work of Hagan *et al.* (1950) on rats and from that of Harrison *et al.* (1952) on a man that fluoroacetate would be removed within a very few days from any animal receiving a sub-lethal dose of 1080.

The levels of 1080 in the livers and hearts of the eight deer were of the same order or less than those in the corresponding meats. The small sizes of these organs would preclude any poisoning hazard to a man eating them. It is considered that the extremely soluble nature of 1080 would make the concentration of the poison in the tissues at death at least as high as, if not higher than, that at the first development of symptoms of poisoning, and hence the results obtained would probably make the toxicity of the tissues appear slightly greater than they would have been when symptoms first appeared. It is possible also that the necessarily delayed autopsies allowed some post-mortem diffusion of the poison to take place, but if this did occur it would certainly have been away from the rumen and towards the tisues examined, making them more toxic at autopsy than at death.

Chronic 1080 poisoning in man has not been reported or suspected, but some data are available for animals. Jarrett and Packham (1956) dosed sheep daily with 1080 at the rate of 0·25 mg/100 g of the whole diet, the poison being given separately from the food. An unspecified number of sheep died in a few (unspecified) days. Other sheep on the same regime died in about twenty days. The sheep failed to eat their full ration of 800 g of wheaten chaff daily after seven to ten days' treatment and had an almost total loss of appetite after twelve to eighteen days. The daily amount of poison administered was kept constant during the whole period. Without going further into this work which showed that the effects of repeated administration of sub-lethal doses of 1080 to sheep were greatly influenced by the nature of the fodder, it is obvious that in sheep there are chronic effects from 1080. Miller and Phillips (1955) found that the inclusion of 2 mg 1080/100 g of the whole diet of young rats caused a marked drop in the growth rate of the rats for the first week with diminishing effects in subsequent weeks. The experiment was run for twelve weeks without deaths occurring. Even when the level of fluoroacetate was doubled after seven weeks and continued at the higher rate for a further five weeks no deaths occurred. On an equal body weight basis the acute fatal dose for sheep is about one-fifth of that for these rats but fatal doses for these rats and man are similar. The level of 1080 in the most toxic deer meat (F) was 0·92 mg/100 g (adjusted analytical figure) and, in the case of man, deer meat alone would not be the sole item of

diet. The relative intake of 1080 by a man eating a meat like F daily could thus not approach the level found harmless in the above experiment on rats. Since there is a great difference in the acute toxicity of 1080 to man and sheep it is considered impossible to assess the possible chronic effects on man of up to 1 mg 1080/100 g of diet, on the basis of the harmful effects on sheep of a diet containing one-quarter this level of the poison. Any considerations are further complicated by the different alimentary systems. Whether or not harmful effects would be expected in a man with such a 1080 intake it would be undesirable that a meat containing this level should be eaten daily for many days. As stated earlier, there would be little opportunity for such meat to be taken for food.

## Conclusions

From the examination of muscle, heart, and liver tissues of eight deer poisoned in a field experiment it is concluded that acute poisoning in a man eating these tissues from a deer poisoned with 1080, at the level used in this experiment, could not occur. The tissues of all the deer examined were contaminated with the poison and are considered unsuitable as food for man. No conclusion can be drawn as to whether prolonged daily intake of meat of the highest toxicity found could in any circumstances be harmful to man. The short time to death in an animal poisoned with a high level of 1080 would make it most improbable that it would be shot for meat. In an animal with a low intake of 1080 and consequent longer survival time, the poison content of the meat is so low that acute toxicity in man would be impossible and chronic toxicity unlikely. An animal eating a non-fatal dose of 1080 would not present any poisoning hazard to a man eating its meat. In the use of 1080 as a poison for deer, efforts should be made to reduce the poison in baits to the lowest level compatible with high percentage kills.

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## References

Hagan, E. C.; Ramsey, L. L.; Woodard, G., 1950: Absorption, Distribution, and Excretion of Sodium Fluoroacetate (1080) in Rats *J. Pharmacol. 99* : 432-4.

Harrison, J. W. E.; Ambrus, J. L.; Ambrus, C. M.; Rees, E. W.; Peters, R. H.; Reese, L C., 1952: Acute Poisoning with Sodium Fluoroacetate (Compound 1080). *J. Amer. med. Ass. 149* : 1520-2.

Jarrett, I. G.; Packham, A., 1956: Response of the Sheep to Sub-lethal Doses of Fluoroacetate. *Nature, Lond. 177* : 580-1.

McGIRR, J. L.; PAPWORTH, D. S., 1955: The Toxicity of Rodenticides. I. Sodium Fluoroacetate, Antu, and Warfarin. *Vet. Rec. 67* : 124-30.

MILLER, R. F.; PHILLIPS, P. H., 1955: Effect of Feeding Fluoroacetate to the Rat. *Proc. Soc. exp. Biol. 89* : 411-3.

PETERS, R. A., 1953: Lethal Synethesis. *Proc. roy. Soc. 140B* : 143-70.

RAMSEY, L. L.; CLIFFORD, P. A., 1949: Determination of Monofluoroacetic Acid in Food and Biological Materials. *J. Ass. off. agric. Chem. Wash. 32* : 788-97.

RUDD, R. L.; GENELLY, R. E., 1956: Pesticides: Their Use and Toxicity. *Calif. Dep. Fish Game, Game Bull. 7* : 137.

# RELIABILITY OF THE COMPRESSOMETER METHOD FOR ANALYSIS OF COARSE WOOLS

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## *Summary*

The applicability of the compressometer method for fleece analysis has been tested, using a range of coarse and variable wools. For finding fibre diameter the method is less accurate than the projection microscope method but it is sufficiently accurate to be used with confidence when groups of fleeces are to be compared. For determination of number of fibres in a sample the method was found to have a level of accuracy comparable to that of the proportionate weight method.


## Introduction

A method of fleece analysis by which mean fibre diameter, the variability of fibre diameter, and the numbers of fibres in a sample can be estimated by first compressing a wool sample from a known area of skin into a slot and making a cast impression of fibres in the slot, has been developed and described by Wilson (1951) and set out in detail by Turner *et al.* (1953). The method has considerable merit because of its simplicity and because the time taken for measurement of fibre diameter is much less than when using the projection microscope. It is also quicker than either the proportionate weight, or other tedious methods, for estimating the number of fibres in a sample.

Original developmental work was done with fine wools in the range 19$\mu$ to 34$\mu$ and nothing has been reported so far concerning the applicability of method to coarser and more variable wools. To test its usefulness with the latter wools a series of 43 individual samples have been measured and compared as described below.

## Materials

The samples used were from a range of stored fleeces mainly from Corriedale and Romney breeds. These wools varied in fibre diameter from 23$\mu$ to 47$\mu$ and the coefficient of variation of fibre diameter ranged from 13·6% to 26·3%.

## Methods

The compressometer used was similar in all important respects to that described by Wilson (1951) and the procedures used in compress-

ing the sample in the slot, polishing and making the cast and counting and calculating followed closely those set out in detail by Turner *et al.* (1953). With untrained operatives some initial trouble was experienced in making successful casts, the difficulty finally resolving itself into one of adequate polishing of the fibre ends immediately before making the cast.

To provide a basis for evaluation of the compressometer method the fibre diameter of each sample was measured, using a standard Reynolds and Branson projection microscope and according to the method set out in the International Wool Textile Organization Draft Specification: "the determination of wool fibre thickness by the projection microscope". A total of 25 fibres was measured on each slide. It is not possible to measure an exact duplicate of the fibres from which the cast is made and some error is thereby introduced. In order to minimize this error fibre snippets to be measured with the projection microscope were taken from the sample immediately adjacent to the level at which the cast was made.

The data have been treated uniformly by calculating correlation and regression coefficients for pairs of observations on the one sample and the standard error of estimate of the regression coefficient has been used as a measure of repeatability of measurement. This measure describes the distribution about the regression line and is similar to but slightly more accurate than the standard deviation of the differences between the pairs of observations within a series.

## RESULTS

### *Repeatability of Measurement of Fibre Diameter using Lateral Projection*

In any comparison it is important to have a measure of the accuracy of the reference method and in the present instance two separate estimates have been made (Table 1). The first was from measurement by the projection microscope of fibres on each of 30 pairs of duplicate slides, each pair prepared from one sub-sample. The second was from repeat measurement of a set of 40 slides. It is widely recognized that there are errors associated with measurement of fibre diameter using the lateral projection method but it has been concluded that these errors are less than those associated with other methods (Palmer, 1951). Providing adequate control has been exercised in sampling of fibres to be measured, the chief error appears to be associated with focussing.

It will be noted that mean differences are satisfactorily small, indicating that valid comparison of groups of sheep could be made. As would be expected, both correlation and regression coefficients are very high. However, the standard error of estimate of the second observation is high in both cases and, as pointed out in the discussion on methods, this is a measure of the distribution of the second measurements about the regression line. It indicates that when duplicate slides

TABLE 1.—Repeatability of Measurement of Fibre Diameter using the Projection Microscope.

| | Duplicate Slides from One Sub-sample | Repeat Measurement of One Slide |
|---|---|---|
| No. of pairs of observations .... .... .... | 30 | 40 |
| Mean difference of second observation ($\mu$) | $+0{\cdot}22$ n.s. | $-0{\cdot}18$ n.s. |
| Correlation coefficient (r) .... .... .... | $0{\cdot}976$** | $0{\cdot}980$** |
| Regression coefficient (b) .... .... .... | $0{\cdot}993 \pm 0{\cdot}041$ | $0{\cdot}951 \pm 0{\cdot}032$ |
| Standard Error of Estimate of second observation ($\mu$) .... .... .... .... | $1{\cdot}23$ | $0{\cdot}86$ |

n.s. = not significant
* probability $< 0{\cdot}05$
** probability $< 0{\cdot}01$

from the one sub-sample are measured for fibre diameter, approximately two-thirds of the second observations are within $\pm 1{\cdot}23\mu$ of the first observation, and when repeat measurements are made on the one slide, approximately two-thirds of the second measurements are within $\pm 0{\cdot}86\mu$ of the first. These errors of estimate appear to be larger than those found by Palmer (1951) when investigating repeatability of measurement of a series of wool tops. However, since approximately 95% of the differences between observations will fall within $\pm$ twice the standard error of estimate, in the case of duplicate slides being measured some 95% of second observations will be within approximately $2{\cdot}5\mu$ of the first and this slightly exceeds one quality interval. This cannot be regarded as very satisfactory and indicates that, for the coarser wools, special precautions need to be taken in mixing the sub-sample and that it would be advantageous to measure more than 250 fibres per slide. Repeat measurements of the one slide are more satisfactory, with approximately 95% of the second observations within $\pm 1{\cdot}7\mu$ of the first.

### *Repeatability of Assessment of Diameter from Cast*

Wilson (1951) has shown that packing is not uniform over the whole area of the cast and has recommended the number and general position of fields to be counted. Error may arise through a regional non-uniformity of fibre size within the cast, through observer error in choosing the most representative area within which to count fibres and through assessment of the packing factor. Observer repeatability in assessment of diameter was tested using one observer who made independent and random duplicate counts on each of the 43 casts. The result, set out in Table 2, shows a very small and non-significant mean diameter difference between observations 1 and 2 and the standard error of estimate of the regression coefficient of $1{\cdot}28\mu$ indicates a de-

gree of repeatability comparable with that obtained when measuring, by lateral projection, duplicate slides prepared from the one sub-sample.

TABLE 2.—Repeatability of Observation of Individual Casts.

| | |
|---|---|
| Number of camparisons .... .... .... .... .... .... | 43 |
| Mean difference in diameter ($\mu$) .... .... .... .... | 0·12 n.s. |
| Correlation coefficient (r) .... .... .... .... .... | 0·964** |
| Regression coefficient (b) .... .... .... .... .... | 1·005 ± 0·044 |
| Standard of error of estimate of second observation ($\mu$) | 1·28 |

*Relationship of Fibre Diameter Found by Lateral Projection and by Cast*

Independent counts were made by three observers on each of the 43 casts and the results so obtained have been compared (Table 3) with the first lateral projection measurements made on the corresponding sample. Observers 1 and 2 had gained some practice with the cast method while observer 3 had had no experience with the technique prior to making observations.

TABLE 3.—Relationship of Fibre Diameter found by Lateral Projection and by Cast for each of Three Observers.

| Observer .... .... .... | 1 | 2 | 3 |
|---|---|---|---|
| Number of comparisons | 43 | 43 | 43 |
| Mean difference cast from lateral projection ($\mu$) .... .... | − 0·10 n.s. | + 0·21 n.s. | 1·03** |
| Correlation diameter by cast and by lateral projection (r) .... | 0·946** | 0·975** | 0·957** |
| Regression of diameter by cast on diameter by lateral projection (b) .... .... .... | 0·821 ± 0·044 | 0·935 ± 0·033 | 0·880 ± 0·042 |
| Standard error of estimate of diameter by cast ($\mu$) .... .... | 1·42 | 1·08 | 1·35 |

Considering first the mean differences, the small differences for observations 1 and 2 approximate the degree of accuracy that can be attained when repeating measurements using the lateral projection method alone. However, the mean difference for observer 3 is highly significant; but this difference would appear to be a consistent one if judged by comparing the correlation coefficients and the standard errors of estimate for observers 1 and 3 in which observer 3 had a slightly

higher correlation between measurements and a slightly lower standard error of estimate. It therefore seems unlikely that inexperience was the chief cause of the high difference and it appears advisable that, if more than one observer is employed, results obtained by the different observers should be routinely checked from time to time. Providing this precaution is observed, it is apparent that comparison of fibre diameter of groups of sheep can be made with confidence using the cast method.

Correlations are high, as would be expected, and the standard errors of estimate of the regression coefficients are comparable with those obtained on repeating counts of one cast and those obtained when measuring by lateral projection duplicate slides prepared from one subsample. One quality interval is approximately $2\mu$ and it can be noted that for observer 1 approximately two-thirds of the measurements are well within one quality interval and 95% within $1\frac{1}{2}$ quality intervals of the measurement obtained with the lateral projection method. In the case of observer 2, approximately 95% of measurements are within one quality interval.

The standard errors of estimate in Table 3 can be considered in relation to those of Table 1. A reduction of the error in measuring fibre diameter by the lateral projection method and on which the regression of measurement by cast is calculated would in most cases reduce the standard error of estimate of cast measurements. The error of measurement by lateral projection reported here is higher than that found in some laboratories. For example, consideration of the data from fourteen laboratories reported by Palmer (1951) suggests that a standard error of estimate of approximately $0{\cdot}5\mu$ would be a reasonable figure for the average minimum error of measurement, although some laboratories reported errors comparable with those found here. In the present comparison there is an added source of error in that exact duplicates, one to be measured by each method, could not be prepared. A small error is thus likely to have resulted from the well-known variation of fibre diameter along the length of the fibre.

### *The Influence of Mean Fibre Diameter on Estimation of Fibre Diameter by the Cast Method*

In Table 4 separate analyses are given for samples with a fibre diameter range of $23\mu$ to $35{\cdot}9\mu$ and for those ranging from $36\mu$ to $47\mu$ as measured by the lateral projection method.

It is evident that the fibre diameter of the sample being measured has no marked influence on the accuracy of determining fibre diameter or on the standard error of estimate associated with regression of diameter by cast on that by lateral projection. In addition it will be noted that the cast estimates of observer 3, which differed significantly when considered as a group, where consistently different whether the wool was fine or coarse. There appears to be nothing in these data to suggest that the procedure evolved by Wilson for fine wools is not equally applicable to coarse wools.

TABLE 4.—Influence of Mean Fibre Diameter on Estimation of Fibre Diameter by the Cast Method.

| | Fibre Diameter | | | | | |
|---|---|---|---|---|---|---|
| | 23μ to 35·9μ (mean 31·9μ) | | | 36μ to 47μ (mean 39·5μ) | | |
| Observer | 1 | 2 | 3 | 1 | 2 | 3 |
| Number of Comparisons | 19 | 19 | 19 | 24 | 24 | 24 |
| Mean difference cast from lateral projection (μ) | + 0·19 n.s. | + 0·34 n.s. | − 0·87** | − 0·32 n.s. | + 0·11 n.s. | − 1·14** |
| Correlation diameter by cast and by lateral projection (r) | 0·928** | 0·964** | 0·951** | 0·726** | 0·895** | 0·770** |
| Regression of diameter by cast on diameter by lateral projection (b) | 0·773 ± 0·075 | 0·980 ± 0·065 | 0·829 ± 0·065 | 0·454 ± 0·092 | 0·700 ± 0·074 | 0·628 ± 0·111 |
| Standard error of estimate of diameter by cast (μ) | 1·27 | 1·11 | 1·11 | 1·11 | 0·90 | 1·34 |

TABLE 5.—Influence of Coefficient of Variation on Estimation of Fibre Diameter by the Cast Method.

| | Coefficient of Variation | | | | | |
|---|---|---|---|---|---|---|
| | Up to 19·9% (mean 17·4%) | | | 20% and greater (mean 22·6%) | | |
| Observer | 1 | 2 | 3 | 1 | 2 | 3 |
| Number of comparisons | 25 | 25 | 25 | 18 | 18 | 18 |
| Mean difference cast from lateral projection (μ) | + 0·12 n.s. | + 0·02 n.s. | − 1·08** | − 0·40 n.s. | + 0·48 n.s. | − 0·94* |
| Correlation diameter by cast and by lateral projection (r) | 0·964** | 0·985** | 0·974** | 0·907** | 0·953** | 0·911** |
| Regression of diameter by cast on diameter by lateral projection (b) | 0·821 ± 0·047 | 0·945 ± 0·035 | 0·900 ± 0·440 | 0·836 ± 0·097 | 0·884 ± 0·071 | 0·815 ± 0·092 |
| Standard error of estimate of diameter of cast (μ) | 1·26 | 0·94 | 1·18 | 1·67 | 1·22 | 1·59 |

*The Influence of Coefficient of Variation on Estimation of Fibre Diameter by the Cast Method.*

Of the 43 samples forming the test series, 25 had, according to lateral projection measurement, a coefficient of variation of less than 20% and the remainder had values of 20% or greater. The errors of estimate for each observer for each of the two groups are given in Table 5.

The errors of estimate for the more variable group are greater, but not significantly so, for all three observers and the trend towards greater error in measuring the more variable wools is exhibited throughout all the data in Table 5. For two out of three observers there is a greater difference between the two methods in mean diameter and, for all three, correlation coefficients are lower and the standard error of the regression coefficients is greater. There appears no reason why results for variable wools could not be improved by counting more than six fields on the cast and by measuring more than 250 fibres per slide. Indeed, this is generally recommended practice when measuring with the projection microscope wools with a high coefficient of variation. However, any increase in accuracy is likely to be small and might be of questionable value where comparison of large groups of fleeces is required.

*Estimation of Coefficient of Variation by the Cast Method*

The coefficient of variation for ten representative casts was determined according to the method described by Turner *et al.* (1953) and is compared in Table 6 with that found for the same samples by lateral projection. It can be noted that agreement is generally good and that the cast method would be sufficiently accurate for comparison of groups.

TABLE 6.—% Coefficient of Variation of Fibre Diameter by Lateral Projection and Cast Methods.

| Number of Sample | 14 | 20 | 24 | 25 | 26 |
|---|---|---|---|---|---|
| Lat. Project | 15·5 | 17·4 | 20·3 | 15·9 | 22·3 |
| Cast | 15·5 | 13·9 | 21·4 | 14·0 | 21·1 |
| Difference | — | −3·5 | +1·1 | −1·9 | −1·2 |
| Sample | 30 | 31 | 36 | 42 | 47 |
| Lat. Project | 17·3 | 15·9 | 15·6 | 25·1 | 24·5 |
| Cast | 17·8 | 17·2 | 13·5 | 29·8 | 25·1 |
| Difference | +0·5 | +1·3 | −2·1 | +4·7 | +0·6 |

*Estimation of Number of Fibres in a Sample by the Cast Method*

Using a group of the coarser wools, a check on the accuracy of estimating numbers was made by manually counting 8 samples from which a cast had been made and from which numbers had been calculated. Numbers in a further group of 12 samples were estimated by the pro-

portionate weight method. Relevant data are in Table 7 and considering first the comparison with the manually counted group it is clear that a very useful estimate of numbers in a sample can be obtained with the cast method. Approximately two-thirds of the estimates are within 5% of the number in the sample and this compares favourably with the error associated with the proportionate weight method (Henderson, 1953). The effect of the latter error is reflected in the much greater standard error of estimate found when the proportionate weight estimate is used as a basis of comparison.

TABLE 7.—Estimation of Number of Fibres in a Sample by the Cast Method.

| | Estimation of numbers by counting | Estimation of numbers by proportionate weight | Combined sample |
|---|---|---|---|
| Number of comparisons | 8 | 12 | 20 |
| Mean number of fibres in sample | 13,660 | 13,290 | 13,440 |
| Mean difference cast estimate | — 450 | — 180 | — 290 |
| Correlation Nos by cast and Nos by — | 0·984** | 0·951** | 0·959** |
| Regression Nos by cast on Nos by — | 0·840 ± 0·064 | 0·881 ± 0·091 | 0·868 ± 0·061 |
| Standard error of estimate of numbers by cast | 660 | 1,490 | 1,190 |

## CONCLUSIONS

The described tests of the repeatability and accuracy of the cast method for measuring fibre diameter have shown that the cast method is not as accurate as the projection microscope method. However, the standard errors of estimate of the regression coefficients show that the method as devised for fine wools is equally applicable to coarse wools and can be satisfactorily and advantageously used when the comparison of groups of fleeces is the prime requirement. Inexperienced observers can provide reproducible results but it is obvious that observers may consistently differ so that frequent inter-observer checks are necessary.

For estimation of numbers of fibres in a sample the method has a great advantage in reducing the time required for the operation and the errors of estimation appear comparable with those obtained by the proportionate weight method which is probably the least tedious of the methods available for estimating numbers in a sample.

On the whole, the standard errors of estimate for fibre diameter by the cast method are higher than those obtained by Ross (1958) when using the Airflow method on a range of wools similar to those used here. In many types of investigation the slight loss of accuracy associated with the cast method may be amply compensated for by the ease of

making observations and the ability to estimate fibre diameter, coefficient of variations of fibre diameter, and numbers of fibres from one cast.

## ACKNOWLEDGEMENT

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## REFERENCES

HENDERSON, A. E., 1953: Fleece Development and Wool Growth on the Romney Lamb *J. agric. Sci. 43* : 12-53.

PALMER, R. C., 1951: Report of the 1948 Inter-Laboratory Diameter and Length Experiment. *J. Text. Inst. 42* : P 23-P 43.

ROSS, D. A., 1958: Rapid Measurement of the Fibre Diameter of Romney Crossbred Wool by the Airflow Apparatus. *N.Z. J. Sci., 1* : 127-42.

TURNER, H. N.; HAYMAN, R. H.; RICHES, J. H.; ROBERTS, N. F.; WILSON, L. T., 1953: Physical Definition of Sheep and their Fleece for Breeding and Husbandry Studies. *Div. Anim. Hlth. Prod. Sci. Res. Org. Canberra. Rep. 4.*

WILSON, L. T., 1951: Physical Analysis of the Fleece of Sheep for Biological Purposes. *Aust. J. agric. Res. 2* : 181-94, 195-204.

# THE EFFECT OF CURING AND SMOKING ON THE QUALITY AND YIELD OF LARD

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**Summary**

An investigation conducted on a strictly comparative basis revealed that the melting point and yield of lard remain unaltered by the curing and smoking processes. Curing increased the acid value and the colour of the dry rendered fat and affected slightly its odour and flavour. The effect of smoking on the odour and flavour of lard was pronounced and deleterious.

## Introduction

Lard is rendered mainly from the hard internal fatty tissues of the pig, but may include also fat from other parts of the carcass. In this connection the advisability of using bacon trimmings for the manufacture of lard has been often discussed and various opinions are held in the bacon curing industry on this subject. In particular there has been a school of thought amongst New Zealand bacon curers that cured bacon yields not only less fat compared with pork fat, but also a product of inferior quality. Further, there seem to be differing opinions regarding the melting points of pork fat and bacon fat. Whereas some curers apparently believe that curing raises the melting point of the fat, others hold just the opposite view. However, several representatives of the bacon industry consulted on this point stated that neither belief has experimental backing, and thought that the clarification of the whole issue would be of considerable interest to the industry.

A preliminary examination of randomly selected pork and bacon fat samples carried out in this laboratory revealed, as could be expected, a variety of melting points and other characteristics. This could explain the conflicting observations previously referred to, and it was obvious that only an investigation carried out on a strictly comparative basis was likely to disclose to what extent the physical and chemical characteristics and the yield of lard are affected by the process of curing and smoking. The present paper reports the results of such an investigation.

## Experimental

The material used in the present work was obtained through the courtesy of Messrs The Kiwi Bacon Co. Ltd., Palmerston North. A shoulder from an excessively fat Wiltshire side was removed, and a thick slice was cut from the shoulder end so that it represented a complete cross-section of the side. This sample, weighing about 2000 g

consisted of approximately 70% adipose tissue and 30% muscle, and was the source of "uncured" fat. The remaining section of the side was pumped with the curing pickle, placed in a brine tank overnight, slightly sprinkled with salt, and stacked with other bacon to mature for 3 weeks. The sample of "cured" fat was obtained by cutting a thick slice (about 2000 g) from the cured material before washing, and represented another complete cross-section of the original side adjacent to the slice removed before curing. The "cured" fat was then divided into 2 equal parts, one of which was smoked, using the procedure described by Watson (1958). The last mentioned sample represented "cured and smoked" fat.

Twenty-five gramme samples of the adipose tissue from "uncured", "cured", and "cured and smoked" material were extracted exhaustively with ethanol and ethyl ether in a soxhlet apparatus. The solution was filtered from fibrous residue and after the evaporation of the solvents the fat was dried *in vacuo*. The melting points of the fats were determined by the Wiley method (Amer. Oil Chemists' Soc. Official and tentative methods). Since it was suspected that the curing process might have resulted in some *cis-trans* isomerization of the unsaturated fatty acids owing to the presence of sodium nitrite in the curing pickle, the examination was extended to the fatty acid portion of the three fats. To this end 3 g samples of each fat were saponified with alcoholic potassium hydroxide and the fatty acids recovered as described by Hilditch (1956). The assay for *trans*-unsaturated fatty acids was carried out by the infra-red technique (Hartman *et al.* 1955), and in addition, melting points, saponification equivalents, and iodine values were determined by the usual methods.

The effect of curing and smoking on the quality and yield of lard was examined by employing a laboratory procedure which followed essentially the "dry" rendering method practised in most New Zealand bacon curing plants. To 100 g samples of finely minced adipose tissue 5 ml of water was added and the mixture heated with stirring in a glycerol bath at 110° C and 130° C respectively for 1 hour. The rendered fat was drained off through a perforated filter, the residue pressed with a spatula to remove as much fat as possible and both fat and residue were weighed. The examination of the fat consisted in determining the acid value, melting point (Wiley method) and colour (in a Lovibond tintometer). Flavour and odour were assessed organoleptically. For comparison the melting point of fatty acids recovered from the fat was determined by the capillary method.

## RESULTS

The data obtained for solvent extracted fats are shown in Table 1, and those for the heat rendered fats in Table 2.

## DISCUSSION

Of several methods of melting point determination tried in the present work, the Wiley method, which is favoured in the United States

for the estimation of melting point of lard, proved most satisfactory. From the data in Table 1 and 2 it is evident that the melting points of fats, whether solvent extracted or dry rendered, are not affected by curing and smoking. This is corroborated by the melting points of the corresponding fatty acids. The assumption that curing and smoking may facilitate the *trans*-isomerization of unsaturated acids was not substantiated (*cf.* Table 1), and can be discounted. Thus, beliefs as to the effect of curing and smoking on the melting points of fats seem to have originated from the comparison of materials inherently different. In fact, the differences in the melting point of fatty acids from randomly chosen uncured and cured fats observed during the preliminary examination, could be traced to the differences in iodine values and neutralization equivalents of the fatty acids.

TABLE 1.—Characteristics of Solvent Extracted Pig Fats and of Fatty Acids Obtained Therefrom.

| | Glycerides | | Fatty acids | | | |
|---|---|---|---|---|---|---|
| Sample | M.p. Wiley ° C | Acid value | M.p. (capillary method) ° C | Iodine value (Wijs) | Neutr. equiv. | *Trans*-acids % |
| Uncured fat | 39·5 | 0·8 | 41·5-42·5 | 53·0 | 270·6 | 3·5 |
| Cured fat | 40·5 | 1·4 | 41·8-42·8 | 53·0 | 272·0 | 3·2 |
| Cured and smoked fat | 39·5 | 1·5 | 41·5-42·5 | 53·5 | 269·7 | 4·4 |

Table 2 shows further that the yield of dry rendered fat is not appreciably affected by curing and smoking, whereas its quality as an edible product is affected to a considerable extent. The acid value of the rendered cured fat is almost twice as high as that of the uncured fat, and this difference is also noticeable in the solvent extracted fats. The colour of the cured and smoked fats is much darker than that of the uncured fat, and in each case depends greatly on the temperature of rendering. Finally, the cured fat is slightly inferior, and the cured and smoked fat greatly inferior to the uncured fat with regard to odour and flavour.

## CONCLUSIONS

The results of the present work lead to the following conclusions:

Trimmings from cured (but not smoked) bacon may be used for the preparation of lard if care is taken to keep the temperature during the rendering process as low as possible. The fat thus obtained is of inferior quality compared with uncured fat, but it could be blended in moderate proportions with prime lard. The rendering of smoked bacon fat should be preferably not attempted, since even small additions of such fat may affect adversely the quality of the bulk product.

TABLE 2—.Characteristics and Yields of Dry Rendered Pig Fats.

| Sample | Glycerides | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Yield | | M.p. Wiley ° C | Acid value | Colour in Lovibond Tintometer 1 inch cell | | Odour and flavour | Fatty acids M.p. ° C (capillary method) |
| | % Fat | % Pressings | | | Yellow | Red | | |
| Uncured fat | | | | | | | | |
| rendered at 110° C | 77·9 | 15·4 | 39·5 | 0·9 | 0·4 | 0·1 | Bland | 41-42 |
| rendered at 130° C | 85·1 | 9·5 | 40·5 | 0·8 | 2·0 | 0·6 | Bland | |
| Cured fat | | | | | | | | |
| rendered at 110° C | 74·6 | 17·1 | 40·0 | 1·4 | 9·7 | 1·5 | Faint | |
| rendered at 130° C | 82·6 | 8·6 | 40·0 | 1·4 | 23·0 | 3·9 | Faint but noticeable | 41·5-42·5 |
| Cured and smoked fat | | | | | | | | |
| rendered at 110° C | 78·4 | 15·6 | 40·0 | 1·5 | 13·0 | 2·5 | Unpleasant | 40·5-41·5 |
| rendered at 130° C | 85·8 | 8·3 | 40·0 | 1·6 | 21·0 | 3·8 | Unpleasant | |

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## REFERENCES

AMERICAN OIL CHEMISTS' SOC.: Official and Tentative Methods, 2nd. edit. Cc 2-38.

HARTMAN, L.; SHORLAND, F. B.; MCDONALD, I. R. C., 1955: The *trans*-Unsaturated Acids Contents of Fats of Ruminants and Non-ruminants, *Biochem. J. 61* : 603.

HILDITCH, T. P., 1956: "The Chemical Constitution of Natural Fats". Chapman & Hall, London, 3rd. edit., p. 572.

WATSON, C. C., 1958: The Contamination of Bacon by Arsenic from Smoke Derived from Preservatized Wood, *N.Z. J. Sci. 1* : 361.

# SOME METHODS OF OBTAINING LARGE SEA-WATER SAMPLES FROM DEPTH

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*(Received for publication, 8 May 1959)*

***Summary***

The construction and operation of three large-capacity sea-water samplers is described. The samplers have been used to obtain large samples for determination of $^{14}C$ activity of sea water.

## Introduction

The following is a description of the methods used by the New Zealand Oceanographic Institute to obtain larger samples of sea water from depth than are provided by conventional apparatus—in particular, to collect a sufficient volume of water for natural radiocarbon analysis. For this purpose from 40 to 80 gallons have been required from depths of up to several thousands of metres.

## Sampler A

Recent papers by Brodie and Burling (1958) and Garner (1958) discussed analyses of samples obtained with this equipment. The capacity of the sampler was 20 gallons contained in four 16-gauge stainless steel tubes each 6 ft 6 in. long and 5 in. diameter. Figure 1 shows the construction and operation of the instrument, which was modified from a design by the Scripps Institution of Oceanography.

The sampler is lowered with the four tubes open at each end. At the required depth a period of at least 10 min. was allowed for flushing before the tubes were closed with their inverted rubber plumber's cups, joined by taut rubber tubing through the length of each tube. The closing gear was triggered by a 19 oz brass messenger dropped down the supporting wire from the surface.

The sampler was drained by gravity through a tap at the bottom of each tube (after opening bleed valves at the top) into a plastic-lined 44-gallon drum (as used for the commercial supply of detergent). Attached to these taps were $\frac{1}{2}$ in. plastic hoses. Successive lowerings were made until the required volume of water was obtained.

A conventional reversing bottle was placed 3 metres above the large sampler; the thermometric depth gave the depth at which the bottle was closed, and a comparison of the salinity of water in the two samplers provided a check against the premature tripping of the large sampler.

Three-sixteenths of an inch diameter stainless steel wire rope of a $3 \times 7$ construction has been used, with a spring accumulator, for lower-

FIG. 1.—Sampler A in open position ready for lowering.

ing the sampler. A bottom weight was used below the sampler only to arrest swinging during heavy rolling. No swivel has been used above the sampler, although this would be an improvement.

When closed, the sampler weight (about 200 lb in air) is taken by the cups sealing the bottom of the tubes; after removal from the water, however, trouble was always experienced with leakage from these

bottom seals due to the tubes being knocked out of shape against the ship's side during recovery of the sampler. Guard rings have recently been fitted but not yet tested in the field.

## SAMPLER B

Trials have been made of a different type of sampler (Fig. 2 (a) and (b)). This consisted of a 30-gallon tank, about 15 in. diameter and

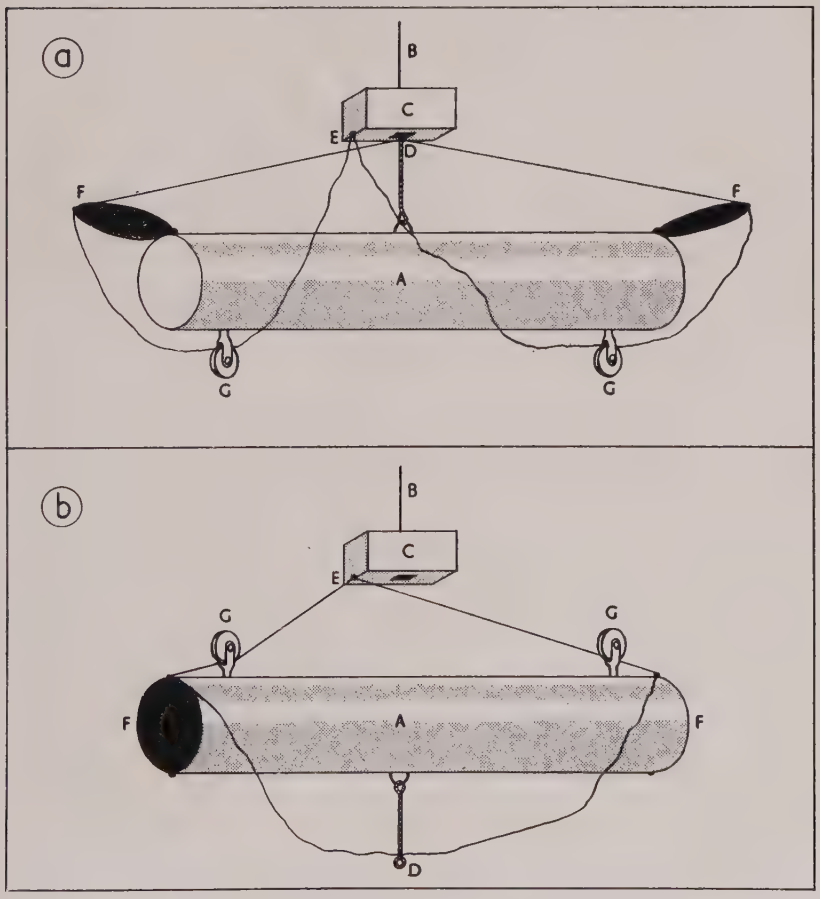


FIG. 2.—Sampler B (a) open, and (b) closed.
A—30-gallon cylindrical tank.
B—wire from winch.
C—modified net release gear.
D—release ring with support wires for sampler and doors during lowering.
E—lifting point for support wires during recovery.
F—hinged doors.
G—pulleys for recovery wires.

4 ft long, made from $\frac{1}{8}$ in. mild steel, with a hinged door at each end. This was supported by a wire rope from a ring which was held in the lowering position by the escape mechanism of a modified plankton net release. Also attached to this ring was a wire trace from each door holding it open. Another trace from each door passed over a pulley and was attached to the fixed part of the release gear. When the release was triggered by messenger, the ring dropped clear, the doors shut, and the sampler turned through 180°. The strain then came on the two traces connected to the main suspension; this held the doors shut as the sampler was hauled to the surface.

This sampler was first drained through hoses but, after trouble with freezing during Antarctic operations, one door was prised open and the contents were poured into an open 44-gallon drum. From this the sample was transferred to the storage drum by bucket during the next lowering of the sampler. A standard reversing bottle was used with this sampler as before, though reversing thermometers could well be fitted inside the tank to give a more positive indication of the depth of sampling.

This sampler was easier to handle and leaked less than the previously described instrument.

## SAMPLER C

This device was the result of an improvization at sea, and was simply a 44-gallon drum with most of the top and bottom removed (Fig. 3). Two lids joined by heavy rubber straps were connected to a net release escape mechanism. A weight was hung from the lower lid. A bridle suspended the drum from the fixed part of the release gear. When triggered, the bottom weight pulled the two lids shut; the length of the rubber strap ensuring that the top lid shut first, and hence that there was tension on both. The water sample was drained into an open 44-gallon drum, and transferred to the storage drum, as before. A thermometer frame could readily be reversed inside this sampler by the closing of the lids. It is intended to use catches on both designs B and C to keep the lids more positively shut until recovery of the sampler.

## SURFACE SAMPLES

Surface samples collected to date have been from the ship's fire main, from an independent pump working over ship's side, or from buckets.

## CONCLUSIONS

Methods based on developments of one or other of the last two designs described here (B and C) seem most promising so far as the sampling requirements of the New Zealand Oceanographic Institute are concerned and further work is being undertaken along these lines.

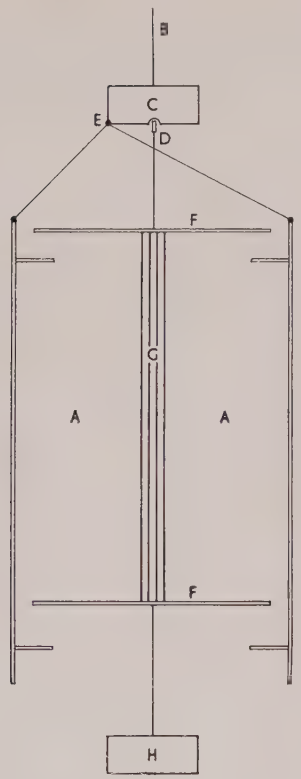


FIG. 3.—Sampler C, open.

A—44-gallon drum.
B—wire from winch.
C—net release gear.
D—release ring.
E—lifting point for support wires during recovery.
F—lids.
G—rubber straps.
H—closing weight.

## ACKNOWLEDGEMENTS

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Sampler B was constructed by Mr A. Atkinson of the Atco Welding and Forging Company of Petone and by A. Langford and D. York of the New Zealand Oceanographic Institute.

Sampler C was due to the ingenuity of J. S. Bullivant, Lieutenant D. A. Christoffel, and the ship's company of H.M.N.Z.S. *Endeavour*, whose improvization permitted the completion of observations after the accidental loss of gear overside.

## REFERENCES

BRODIE, J. W., BURLING, R. W., 1958: Age Determination of Southern Ocean Waters. *Nature 181* : 107.

GARNER, D. M., 1958: A Radiocarbon Profile in the Tasman Sea. *Nature 182* : 466.

# MICRO-DISTRIBUTION OF PLANKTON

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*(Received for publication, 27 May 1959)*

***Summary***

A sampling frame has been constructed to take simultaneously 24 plankton samples of 800 ml volume, at spatial intervals of 10 cm in a horizontal plane. Tests of departure from randomness of sample counts are applied. *Coscinodiscus gigas*, with a mean of over 50 cells per sample is highly over-dispersed, but non-randomness cannot always be detected in zooplankton species, where the mean is in all cases less than 3. It is concluded that over-dipersion is likely to be present in any plankton population, regardless of the spatial scale at which it is investigated, but that where the mean is less than unity it will commonly be necessary to take several hundred samples before significant departure from random can be detected. Further research should preferably be directed toward the casual factors inducing aggregation rather than to the detection and description of non-random patterns.

## Introduction

The term "micro-distribution" has previously been introduced (Cassie, 1959) and arbitrarily defined as the pattern of distribution of plankton in space which will be detected by sampling at intervals of less than 1 metre. It has also been predicted that some difficulties will arise in the statistical handling of data with such a small sample interval, owing to the need for small samples with correspondingly small numbers of individuals per sample. On the other hand, in view of the almost universal phenomenon of non-randomness in plankton distribution as seen in convential sampling on a larger spatial scale, it would seem desirable to have some knowledge of the pattern within a smaller frame of space than is normally studied. Just how small this frame may be will be conditioned to some extent by the practical considerations of field technique, but will depend also on the lower limit set by the abundance of the organisms concerned. It is clear, for instance, that a parcel of water must contain more than one plankter before any "pattern" will be present.

There is, however, a fundamental physical property of natural waters which may also have some bearing on the smallness of pattern which may profitably be investigated. Lieberman (1951) has shown that oceanic waters are surprisingly lacking in physical homogeneity as judged by accurate temperature measurements. Fluctuations with an amplitude and length in the order of 0·1° C and 60 cm respectively are apparently of common if not universal occurrence, at least in the upper 60 metres of the sea. It has also been shown from a field experiment (Cassie, 1959) that there is reason to suspect that some plankters may be sensitive to changes of temperature of this order. While it is

not as yet certain what temperature gradients are involved in those particular experiments it is at least unlikely that they are steeper than those to be expected from the Liebermann effect. For the present experiment a sampling interval of 10 cm was chosen, as being sufficiently less than 60 cm to reveal any reaction to small-scale physical inhomogeneity.

In view of the technical problems of statistical analysis it has been necessary to seek plankton populations which are perhaps not entirely "typical", but which are sufficiently dense to produce adequate sample counts. On 25 September 1957, at Karara Bay, Port Fitzroy, Great Barrier Island (lat. 36° 10·9′ S, long. 175° 21·4′ E) a pronounced bloom of the large solitary diatom *Coscinodiscus gigas* provided a suitable population. On subsequent examination of the material a few species of zooplankton were also found to be present in numbers adequate for randomness tests, and these together with *Coscinodiscus* provide the basis of this paper.

## Apparatus and Field Technique

The apparatus consists of 24 "32 oz" preserving jars arranged in a row on a steel reversing frame 2·4 metres (8 ft) long. A hinged lid lined with sponge rubber and serving all the jars is arranged to remain open when the apparatus is inverted. The spacing of samples is determined by the external diameter of the jars which is almost exactly 10 cm (4 in.). The frame is lowered with jars inverted, relying on the pressure of the enclosed air to exclude water until the moment of campling. On the present occasion the apparatus was used within about 50 cm of the surface so that the effect of water pressure in reducing the volume of air was negligible. After allowing a few minutes for any water disturbances produced by lowering the frame to settle down, the entire assembly is overturned by means of a messenger release, similar in principle to that used on a closing plankton net. The hinged lid is then free to close by gravity over the mouths of the jars. The apparatus is then raised and the contents of the jars transferred by siphoning to holding jars numbered in the same serial order as those in the sampler. A small amount of water is discarded from each jar to compensate for minor spillage and bring the sample volume to a constant 800 ml. The subsamples are then preserved by adding 40 ml of formalin. Plankton is later extracted by sedimentation and total counts made by standard methods.

## Results

Four samples, each of 24 subsamples were taken, Nos 1 and 2 at 2100 and 2130 hr, Nos 3 and 4 at 2300 and 2330 hr respectively. The night was calm and clear with a light south-west breeze. The surface of the bay was smooth, and a tide stream of less than $\frac{1}{4}$ knot was running.

The sample counts are presented in Table 1. Only those species have been recorded which have a mean per subsample of one or more for at

TABLE 1.—Sample Counts, Means, Variances, and Test of Dispersion.

| Sample | *Paracalanus* 3 | *Paracalanus* 4 | *Corycaeus* 3 | *Corycaeus* 4 | *Oithona* 3 | *Oithona* 4 | Nauplii 1 | Nauplii 2 | Nauplii 3 | Nauplii 4 |
|---|---|---|---|---|---|---|---|---|---|---|
| Subsample | | | | | | | | | | |
| 1 | 3 | — | 2 | — | | — | | 4 | 1 | — |
| 2 | | 1 | 4 | 2 | | | 2 | 2 | | 1 |
| 3 | 1 | 1 | 1 | 2 | | | | 3 | 1 | |
| 4 | | 2 | 1 | | 2 | | | 2 | | |
| 5 | 4 | | 2 | 3 | | | 2 | 1 | | |
| 6 | 1 | | 1 | 2 | 1 | | | 2 | 1 | 1 |
| 7 | | 1 | 2 | 1 | 1 | | 2 | 2 | 1 | 1 |
| 8 | 1 | 2 | | 2 | 2 | | | | | 2 |
| 9 | 1 | | | 4 | 1 | | 1 | | 2 | 2 |
| 10 | | 3 | | 1 | 2 | 3 | | | 2 | 2 |
| 11 | 1 | 2 | 2 | 2 | | 3 | | 1 | | |
| 12 | | 1 | 1 | 1 | 1 | 1 | | | | |
| 13 | 3 | 2 | 2 | 1 | 3 | 2 | | 1 | 2 | |
| 14 | 1 | | 1 | 3 | 2 | 1 | | 1 | 1 | 1 |
| 15 | | | 2 | 1 | 1 | 1 | | 2 | | |
| 16 | | 2 | 1 | 5 | 1 | | 1 | 1 | 1 | 2 |
| 17 | | 2 | | 2 | 1 | 2 | | 2 | 3 | 3 |
| 18 | 2 | | 1 | | 1 | 1 | 2 | 2 | 2 | 3 |
| 19 | | | 1 | | 2 | | | | | 1 |
| 20 | 3 | | | | 2 | 2 | 1 | | 1 | 1 |
| 21 | | 2 | | | 1 | | — | 1 | 2 | |
| 22 | 2 | 1 | 2 | | | | — | 2 | 4 | |
| 23 | 1 | 1 | 3 | 1 | | | — | | | |
| 24 | 3 | | 4 | 3 | 1 | 1 | — | | 1 | 4 |
| $\bar{x}$ | 1·12 | 1·00 | 1·38 | 1·57 | 1·04 | ·74 | ·55 | 1·21 | 1·04 | 1·04 |
| $s^2$ | 1·59 | ·86 | 1·38 | 1·89 | ·74 | 1·02 | ·68 | 1·21 | 1·17 | 1·41 |
| $d$ | 1·42 | ·86 | 1·00 | 1·20 | ·71 | 1·38 | 1·24 | 1·00 | 1·12 | 1·36 |
| $c$ | ·37 | — ·14 | ·00 | ·13 | — ·55 | ·51 | ·43 | ·00 | ·12 | ·34 |
| $\chi^2$ | 2·82 | 2·50 | 4·13 | 11·48* | 4·95 | 11·80** | ·82 | 7·62 | 5·57 | 5·14 |
| d.f. | 4 | 3 | 5 | 5 | 4 | 2 | 1 | 4 | 4 | 3 |
| $P <$ | ·7 | ·5 | ·7 | ·05 | ·3 | ·01 | ·5 | ·2 | ·3 | ·2 |

least one subsample, but 0·5 or more is accepted for the remaining samples of the same species. The following species have thus been selected:

| | |
|---|---|
| *Paracalanus parvus* copepodites | (Copepoda) |
| *Corycaeus aucklandicus* | (Copepoda) |
| *Oithona similis* | (Copepoda) |
| Nauplius larvae | (Copepoda) |
| *Oikopleura* sp. | (Appendicularia) |
| *Polydora* larva | (Polychaeta) |
| Medusa larva | (Coelenterata) |
| *Coscinodiscus gigas* | (Diatomales) |

Owing to accidents in handling, sample 1 has been reduced to 20 subsamples, and sample 4 to 23 subsamples for the zooplankton. At the

| *Oikopleura* | | *Polydora* | | | Medusa | | | *Coscinodiscus* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 3 | 4 | 1 | 3 | 4 | 1 | 2 | 4 | 1 | 2 | 3 | 4 |
| | — | | | — | 1 | 1 | — | 16 | 64 | 44 | 48 |
| | 1 | 1 | 5 | 1 | 1 | | 3 | 76 | 64 | 59 | 54 |
| | 3 | | 7 | 5 | | 4 | 1 | 34 | 54 | 24 | 49 |
| | | | 1 | 3 | 1 | 2 | | 47 | 74 | 59 | 88 |
| 4 | 1 | 3 | 2 | 1 | 2 | 1 | | 69 | 24 | 58 | 55 |
| | 3 | | 1 | 3 | | | 6 | 107 | 35 | 83 | 49 |
| 4 | 2 | | 2 | 3 | | 3 | 4 | 77 | 48 | 79 | 86 |
| 1 | 1 | | 5 | 2 | 1 | 2 | | 85 | 86 | 109 | 52 |
| | 1 | | 2 | 6 | 1 | 3 | 1 | 73 | 75 | 87 | 70 |
| | 1 | 2 | 2 | 5 | 1 | | 2 | 89 | 40 | 78 | 49 |
| | | | | 2 | 2 | 1 | 1 | 92 | 27 | 92 | 23 |
| | 2 | 2 | 1 | 2 | 1 | 1 | 3 | 118 | 77 | 129 | 44 |
| 1 | | | 1 | 3 | | 2 | | 81 | 57 | 76 | 93 |
| 1 | | | | 5 | | 1 | 1 | 59 | 79 | 89 | 49 |
| | | 1 | 4 | 2 | 1 | | 2 | 99 | 66 | 105 | 90 |
| | 2 | 3 | 6 | 4 | 2 | 1 | 1 | 109 | 84 | 95 | 72 |
| 2 | 2 | | 4 | 2 | 5 | 4 | 8 | 92 | 70 | 89 | 55 |
| | 1 | | | 5 | 5 | 2 | 1 | 49 | 74 | 102 | 79 |
| 1 | 2 | 1 | 4 | 2 | 1 | 1 | 2 | 90 | 63 | 115 | 52 |
| 4 | | 2 | 2 | 3 | | | | 92 | 64 | 105 | 51 |
| 1 | 1 | — | 4 | 1 | — | | 1 | — | 94 | 113 | 50 |
| | 2 | — | 4 | 2 | — | 1 | | — | 73 | 32 | 64 |
| 2 | 1 | — | 6 | 1 | — | 1 | 1 | — | 41 | 94 | 30 |
| 1 | | — | | 2 | — | 4 | | — | 56 | 86 | 58 |
| ·92 | 1·13 | ·75 | 2·62 | 2·83 | 1·25 | 1·46 | 1·65 | 77·7 | 62·0 | 83·4 | 58·8 |
| 1·82 | ·94 | 1·14 | 4·77 | 2·24 | 2·09 | 1·74 | 4·15 | 674·0 | 344·0 | 693·7 | 416·7 |
| 1·98** | ·83 | 1·52 | 1·82* | ·79 | 1·67* | 1·19 | 2·52** | 8·7** | 5·5** | 8·3** | 7·1** |
| 1·06 | — ·15 | ·69 | ·31 | — ·07 | ·54 | ·13 | ·92 | ·10 | ·07 | ·09 | ·10 |
| 3·09 | 1·54 | ·60 | 16·43 | 4·26 | 9·60* | 1·17 | 12·25** | 165** | 128** | 191** | 129** |
| 3 | 3 | 1 | 11 | 10 | 4 | 5 | 6 | 19 | 23 | 23 | 23 |
| ·5 | ·7 | ·5 | ·2 | ·95 | ·05 | ·95 | ·01 | ·001 | ·001 | ·001 | ·001 |

bottom of Table 1 the means and variances of samples are given, together with other statistics which will be discussed.

## Discussion

Four basic methods are available for testing departure from randomness in samples: goodness of fit to Poisson; index of dispersion; autocorrelation coefficient; and distance to nearest neighbour. Discussion is confined to the first three, since the exact location of individuals within the sample volume is not known.

Perhaps the most critical test when comparatively large numbers of sample counts are available is goodness of fit to a Poisson series based on the sample mean. There is little point in applying this test to *Coscinodiscus* since departure from random is so pronounced as to be

beyond all doubt, but this is not the case with the zooplankton which are much less abundant. Table 2 shows the observed and the expected Poisson frequencies for medusae in samples 1 and 4. It will be seen that agreement is fairly good, even though there is a slight tendency for the higher counts to exceed expectation. The $\chi^2$ test for goodness of fit tends to be biased for small expected numbers, and for this reason it is necessary to pool the frequency data in the tail of the distribution to obtain expected frequencies of 5 or more. In neither case is $\chi^2$ significant.

TABLE 2.—Medusae fitted to Poisson Series.

| Sample 1 | | | | | Sample 2 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| $X$ | $f$ | $\hat{f}$ | | $\chi^2$ | $X$ | $f$ | $\hat{f}$ | | $\chi^2$ |
| 0 | 6 | 5·73 | | ·01 | 0 | 7 | 4·41 | | 1·52 |
| 1 | 9 | 7·16 | | ·47 | 1 | 8 | 7·28 | | ·07 |
| 2 | 3 | 4·48 | | | 2 | 3 | 6·01 | | 1·51 |
| 3 | — | 1·86 | | | 3 | 2 | 3·31 | | |
| 4 | — | ·58 | 7·11 | ·13 | 4 | 1 | 1·37 | | |
| 5 | 2 | ·15 | | | 5 | — | ·45 | | |
| >5 | — | ·04 | | | 6 | 1 | ·12 | 5·30 | ·02 |
| | | | | | 7 | — | ·03 | | |
| | | | | | 8 | 1 | ·006 | | |
| | | | | | >8 | — | ·014 | | |
| | 20 | 20·00 | | 1·11 | | 23 | 23·00 | | 3·12 |
| | $P = 0·57$ (2 d.f.) | | | | | $P = 0·37$ (3 d.f.) | | | |

$X$ = number of medusae per subsample
$f$ = observed frequency of $X$
$\hat{f}$ = expected frequency of $X$ (Poisson)

Two more or less equivalent indices of dispersion are available for which confidence limits may be assigned, the results of both tests being entered at the bottom of Table 2. To the first, commonly known as (Fisher's) coefficient of dispersion we will assign the symbol $d$

$$d = s^2/\bar{x} \qquad \text{..... (1)}$$

where $\bar{x}$ is the sample mean and $s^2$ the variance. If the distribution is Poisson $d$ will equal unity. Greater values indicate overdispersion (aggregated distribution) and lesser values underdispersion (even distribution). The variance of $d$ is $2n/(n-1)^2$ and departure from randomness is considered significant when

$$| d-1 | \geqq t \sqrt{(2n)/(n-1)} \qquad \text{..... (2)}$$

where $n$ is the number of samples and $t$ is drawn from Student's $t$ distribution. Over and underdispersion will be indicated by positive and negative values respectively of this expression. Commonly $t$ is given the value 2, which is a close approximation (when $n > 20$) for the $P = 0·05$ significance level, but other fiducial limits can also be set from table of $t$.

An alternative coefficient of dispersion employs the $\chi^2$ distribution (Fisher, 1925)

$$\chi^2 = (n-1)s^2/\bar{x} \quad (n-1 \text{ degress of freedom})$$
$$= (n-1)d \qquad \ldots\ldots\ldots (3)$$

Since tables of significance levels of $\chi^2$ for up to 30 degrees of freedom are readily available, this statistic is rather more convenient to use. (In the Poisson test above, and Table 2, the $\chi^2$ test was employed in a slightly different manner. For Tables 1, 3, and the remainder of this section, $\chi^2$ will refer to the second application, as an index of dispersion.) It will be noted that, while $\chi^2$ and $d$ are equivalent statistics, the tests of significance do not produce identical results.

For example, when $n = 24$ and $P = 0{\cdot}05$.

$$d = 1 \pm 2{\cdot}064\sqrt{48/23}$$
$$= 1{\cdot}623,\ 0{\cdot}377$$
$$\text{but } \chi^2/(n-1) = 25{\cdot}172/23,\ 13/091/23$$
$$= 1{\cdot}429,\ 0{\cdot}569$$

Thus the $\chi^2$ test will result in rejection of the hull hypothesis (randomness) more often than the $d$ test. However, in the present data, the discrepancy is negligible. The relationship between the two indices is almost constant for sample numbers greater than 10, e.g. when $P = 0{\cdot}05$

$$(1-d) = 1{\cdot}18\ \chi^2/(n-1) \qquad \ldots\ldots\ldots (4)$$

Referring to Table it will be seen that, except for *Coscinodiscus*, the tests of significance are not comparable on the basis of equation (3) because, for $\chi^2$, data have been grouped to provide for expected numbers greater than 5. Significance levels are indicated by asterisks

$$*,\ P < 0{\cdot}05$$
$$**,\ P < 0{\cdot}01$$

For *Coscinodiscus* both tests reveal significance at the higher level, as might have been expected from the very large excess of variance over mean. However, for the zooplankton, although both the $d$ and $\chi^2$ tests show significanc in 4 samples, only in two cases do the samples coincide. These two (Medusae, 1 and 4) are the same samples which showed no evidence of overdispersion in the Poisson test. In four cases $d < 1$, showing a tendency to underdispersion, though the significance level is not approached. However, both Polychaetes (4) and Medusae (2) give $P(\chi^2)$ between 0·90 and 0·95 which verges on significance. On the other hand, for Medusae (2) $d > 1$, thus tending to contradict the $\chi^2$ test.

The general impression gained from the data as a whole is that while *Coscinodiscus* is undoubtedly highly aggregated, the numerical

abundance of the zooplankton is sometimes insufficient to give clear tests of significance even if some departure from random is in fact present. In some instances a visual impression of aggregation is gained from Table 1 even when this is not revealed by the statistical tests.

Thus, *Corycaeus* (3) and Nauplii (2) both appear to have an irregular periodicity even though $d$ is in both cases exactly unity.

An approach to the problem of the size and number of subsamples required to show non-randomness may be made with the aid of the statistic $c$ which is also shown in Table 1.

$$c = (s^2 - \bar{x})/\bar{x}^2 \qquad \text{..... (5)}$$

This is equivalent to the equation relating the mean and variance of a negative binomial distribution.

$$\sigma^2 = m + \gamma m^2 \qquad \text{..... (6)}$$

where $\sigma^2$ = population variance, $m$ = population mean, $\gamma$ = a constant, of which $c$ is the sampling estimate. It is not possible to demonstrate that every plankton population can be described by the negative binomial model, or that $\gamma$ is constant for a given population, regardless of sampling pattern. However, it does in fact appear from the literature that the estimate, $c$, has some measure of stability, and that similar values can be obtained for many plankton populations under some variety of sampling conditions. Barnes and Marshall (1951) tabulate 18 estimates for different populations, ranging from 0·05 to 0·95 (omitting one aberrant group of teleostean eggs where $c$ was 1·8) with a mean of 0·12. Silliman (1946) obtained a mean of 0·11 for pilchard eggs, and Winsor and Walford (1936) 0·05 for various plankton species. Comita and Comita (1957) give values ranging from 0·05 to 0·16 for freshwater copepodid larvae. Although Tonolli (1949) does not give estimates of $c$, these can be computed from his data. In the 82 dominant groups (i.e. species divided into males, females, and juveniles) the range is from $-0{\cdot}89$ to 0·75, with a mean of 0·08. In general, it would seem that a typical value of $c$ is 0·1 and that values greater than unity are of less frequent occurrence, a fact which may be verified from Table 1.

While this information lacks precision, it would appear to be the best available for the purpose of predicting sampling requirements for present purposes.

$c$ and $d$ are related by the equation:

$$c\bar{x} = d - 1$$

Thus, for significance (from equation 2):

$$|\, c\bar{x} \,| \geq t\sqrt{(2n)/(n-1)}$$

Since the detection of overdispersion is only a problem when $c$ and $\bar{x}$ are both small, we may solve for $n$ in the special case where

$$c\bar{x} \leqslant 1$$
$$n = 2t^2/c^2\bar{x}^2 + 2 \quad \ldots\ldots\ldots (7)$$

Thus, for significant departure from randomness ($P = 0{\cdot}05$) to be shown, the number of samples will be:

$$n = 8/c^2\bar{x}^2 + 2$$

For example, when $\bar{x} = 1$, $c = 0{\cdot}1$,

$$n = 802$$

Alternatively, when $\bar{x} = 1$, $n = 24$
$c = 0{\cdot}6$

It is clear, then, that unless relative overdispersion or underdispersion is higher than average, it is not likely to be detected by the $d$ test unless the subsample is sufficiently large for the mean to exceed unity, or a fairly large number of samples is taken. Since the nature of the present investigation requires small-volume samples, the only alternative is to take a number of samples in the order of several hundred. Thus, it is not at all surprising that, of the scarcer species, only a small number of samples show significant departure from random.

TABLE 3.—Zooplankton, Distribution of $P$ ($\chi^2$)

| $P$ | $f$ | $\hat{f}$ |
|---|---|---|
| 1 –·98 | — | ·36 |
| ·98–·95 | — | ·54 |
| ·95–·9 | 2 | ·9 |
| ·9 –·8 | — | 1·8 |
| ·8 –·7 | — | 1·8 |
| ·7 –·5 | 3 | 3·6 |
| ·5 –·3 | 4 | 3·6 |
| ·3 –·2 | 2 | 1·8 |
| ·2 –·1 | 3 | 1·8 |
| ·1 –·05 | — | ·9 |
| ·05–·02 | 2 | ·54 |
| ·02–·01 | — | ·18 |
| ·01–·0 | 2 | ·18 |
| | 18 | 18·00 |

To give some idea of the overall departure from random the distribution of $P$ ($\chi^2$) for zooplankton is tabulated in Table 3. It will be seen that there is a general tendency toward an excess of low values of $P$. The numbers are too small to make a detailed test of significance, but the frequencies above and below $P = 0{\cdot}5$ may be grouped, giving 5 and 13 respectively, for which $\chi^2$ is 3·556 and $P = 0{\cdot}06$. Thus, it may be suspected that when a 10 cm sample interval is used overdispersion is rather more common than underdispersion in the population sampled.

The third or autocorrelation test, while not sensitive to all types of non-randomness, provides a useful supplementary test in that it utilizes not only the sample counts, but also the order in which the sample counts occur. It will be obvious that if a series of random numbers are arranged in some systematic order of magnitude, they will cease to be random, but that none of the previous tests will reveal this fact. Such an extreme case is unlikely to occur in nature but there are, nevertheless, instances where a non-random sequence of numbers is lost sight of by disregarding the order in which they occur. Nauplii (2) may in fact be such a case; $d$ is exactly unity, and $P$ ($\chi^2$) is slightly more than 0·1, neither test revealing significant non-randomness. On the other hand, if we correlate the two subsample series, 1–23 and 2–24 we obtain the correlation coefficient $r = 0{\cdot}39$, with 21 degrees of freedom. This falls just short of the 0·05 significance level ($r = 0{\cdot}41$), suggesting that the numerical density in any one subsample is not entirely independent of that in neighbouring subsamples. Similarly, in Medusae (1), $r = 0{\cdot}50$, which is significant at the 0·05 level, although in this case non-randomness had already been detected by the previous tests.

As suggested in the introduction, aggregation on the micro-distribution scale may have some connection with the temperature fluctuation pattern. Obviously it would be desirable to know the actual temperatures at the time of sampling, but in the absence of these, use must be made of the general form given by Liebermann (1951). This may be described empirically by the correlogram in which the correlation coefficient decreases exponentially to a value of $1/e$ at a distance of 60 cm. At 10 cm intervals successive values of $r$ would then be 0·85, 0·72, 0·61, 0·51, 0·45. For 24 observations the first 4 (i.e. 40 cm) would be significant at the 0·05 level. If the micro-distribution were dependent entirely on the temperature pattern it would be expected that sample counts would produce an identical correlogram. In fact, the variance of plankton will probably have more than one component. Part will be due to chance, part to temperature variation, and part to other unknown factors. However, provided about a quarter of the variance is attributable to temperature, at least the first autocorrelation coefficient will still be significant:

$$\sqrt{(0{\cdot}85^2/4)} = 0{\cdot}42$$

It has already been shown that autocorrelation at about this level is present in two of the zooplankton samples, but the situation is by no means general. For *Coscinodiscus* the first autocorrelation coefficient for samples to 4 is respectively 0·23, 0·17, 0·03, and −0·14, none of which is greater than would be expected to occur by chance. Thus, the effect of minor temperature fluctuation must for the time being remain unresolved. However, it is hoped that a suitable technique will be evolved by which accurate temperatures may be recorded simultaneously with the taking of plankton samples.

## MESO-DISTRIBUTION

While not strictly relevant to the main topic, it is of interest to note the fluctuations in density of plankton with time and space on an intermediate scale (i.e. the meso-distribution). The tidal stream might be expected to bring an appreciable change in the plankton population, while diurnal migration might also have some influence, particularly between the earlier and later pairs of samples. The total sample counts and $\chi^2$ (corrected for unequal numbers of subsamples) are given in Table 4. Within pairs of samples, *Coscinodiscus*, as might be expected, shows heterogeneity of an even higher order than between subsamples of one sample. (Since in Table 4, $\chi^2$ has only one degree of freedom it is appropriate to compare it with $d$ in Table 1). Between pairs, $\chi^2$ does not quite reach significance. While this unusually low value is probably due to chance, it does at least suggest that there has been no change in the *Coscinodiscus* population due to vertical migration.

Within pairs the zooplankton appear to be rather more homogeneous between samples 3 and 4 than between samples 1 and 2. However, the most significant fact would seem to be the pronounced rise in numbers between the earlier and the later sample pairs. This is almost certainly attributable to the upward migration of zooplankton which commonly occurs during the hours of darkness.

TABLE 4.—Between Samples $\chi^2$ Test.

| | *Paracalanus* | *Corycaeus* | *Oithona* | Nauplii | Appendicularia | Polychaetes | Medusae | *n* (zooplankton) | *Coscinodiscus* | *n* (*Coscinodiscus*) |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 7 | — | 11 | 6 | 15 | 25 | 20 | 1554 | 20 |
| 2 | 1 | 2 | — | 29 | 5 | 3 | 35 | 24 | 1489 | 24 |
| $\chi^2$ | — | — | — | 5·24* | ·37 | 10** | ·35 | | 38·7** | 23 |
| 3 | 22 | 33 | 25 | 25 | 22 | 63 | 8 | 24 | 2002 | 24 |
| 4 | 23 | 36 | 17 | 24 | 26 | 65 | 38 | 23 | 1410 | 24 |
| $\chi^2$ | ·09 | ·31 | 1·2 | 0·0 | ·52 | ·18 | 20·5** | | 102** | |
| 1 + 2 | 3 | 9 | — | 40 | 11 | 18 | 60 | 44 | 3043 | 44 |
| 3 + 4 | 45 | 69 | 42 | 49 | 48 | 128 | 46 | 47 | 3412 | 48 |
| $\chi^2$ | 33·1** | 42·4** | 39·4** | ·41 | 20·9** | 73·2** | 1·06 | | 3·78 | |

## DISCUSSIONS AND CONCLUSIONS

The above results have shown that an aggregated pattern may be present in the distribution of plankton even within the very small spatial frame covered by a 10 cm sampling interval. When the sample mean is less than unity, a departure from random may not be detected

except with a large number of samples (perhaps several hundred). Thus, failure of tests of significance may signify insufficient data rather than true randomness. Under-dispersion is either less common or less often detected than over-dispersion. This seems to be in agreement with the results of most workers, both in marine and freshwater environments, e.g. Barnes & Marshall (1951), Ricker (1937), Baldi, Cavalli & Pirocchi (1945), Tonolli (1949 and 1958). On the other hand Comita and Comita (1957) report a predominance of under-dispersion in the freshwater copepod *Diaptomus siciloides*, provided each growth stage is enumerated separately. Unfortunately they do not give any indication of the numerical abundance in their samples of the species concerned. However, a set of counts used in calibrating their sampler, having a mean in the thousands range, is very highly over-dispersed. Only one worker, Lauff (1953), appears to have employed a small sample interval comparable to that used here. His multiple sampler, operating on a piston system, takes 16 samples the volume of which can be varied between 14 and 22 ml. The cylinders are in four rows of four at about 5 cm intervals. His results from a freshwater pond also suggest a predominance of over-dispersion and indicate aggregation on an even smaller spatial scale than has been detected in the present work.

Although no direct causal relation has been shown between aggregation and minor water inhomogenities, it would seem that the possibility deserves further attention, if suitable sampling techniques can be devised.

The main conclusion from this investigation must of necessity be a negative one. The "null hypothesis" that plankton are randomly distributed in space has been rejected for certain species, at a scale of sampling which is smaller and more detailed than has been employed in the majority of previous investigations. Although the test for non-randomness has failed in some instances, there is sufficient evidence to show that a random distribution can never be assumed in advance in any investigation, regardless of the spatial scale being considered. This conclusion has been reached before, by other workers, for less closely-spaced sampling intervals, so that the present work merely extends the range of their findings to the "micro-distribution" level. While under-dispersion is undoubtedly present in certain plankton populations, over-dispersion (where variability is greater than expectation) is probably more commonly encountered and is certainly the greater problem to the ecologist.

Considering more particularly the case of over-dispersion, two important corollaries arise from the general conclusion. Firstly, in sampling as a means of estimating plankton abundance, provision should always be made for estimating sampling error, since the distribution will not necessarily follow the Poisson model, and variance is likely to be greater rather than less than expectation. Secondly, in the study of plankton behaviour, the role of chance in determining micro-distribution may be considerably less than the planktologist is sometimes led by his intuition to expect. Indeed, the presence of a plankter in a particular parcel

of water may be no more "random" than is the presence of a centipede under a log, or a plant growing in a pocket of soil between rocks. While the detection of departure from randomness and the fitting of non-Poisson frequency distribution models may serve a useful purpose in describing empirically the spatial pattern of plankton, it would seem desirable to pay more attention in the future to the physical and biological factors producing departure from randomness.

## REFERENCES


BALDI, E.; CAVALLI, L. L.; PIROCCHI, L., 1945: Condizioni della Distribuzione del Mesoplancton nel Pelago di un Grande Lago Oligotrofo (Lago Maggiore). *Mem. Ist. ital. Idrobiol. de Marchi 2* : 253-89.

BARNES, H.; MARSHALL, S. M., 1951: On the Variability of Replicate Plankton Samples and Some Applications of "Contagious" Series to the Statistical Distribution of Catches Over Restricted Periods. *J. Mar. biol. Ass. U.K. 30* : 233-63.

CASSIE, R. M., 1959: An Experimental Study of Factors Inducing Aggregation in Marine Plankton. *N.Z. J. Sci. 2* : 339-65.

COMITA, G. W.; COMITA, J. J., 1957: The Internal Distribution Patterns of a Calanoid Copepod Population and a Description of a Modified Clarke-Bumpus Plankton Sampler. *Limnol. Oceanogr. 2* : 321-32.

FISHER, R. A., 1925: "Statistical Methods for Research Workers". Oliver and Boyd, Edinburgh.

LAUFF, G. H., 1953: The Design and Application of a Multiple Sample Plankton Trap. Thesis presented for the degree of Doctor of Philosophy, Cornell University.

LIEBERMANN, L., 1951: Effect of Temperature Inhomogeneities in the Ocean on Propagation of Sound. *J. acoust. Soc. Amer. 23* : 563-70.

RICKER, W. E., 1937: Statistical Treatment of Sampling Processes Useful in the Enumeration of Plankton Organisms. *Arch. Hydrobiol. (Plankt.) 31* : 68-84.

SILLIMAN, R. P., 1946: A Study of Variability in Plankton Townet Catches of Pacific Pilchard (*Sardinops caerulea*) eggs. *J. Mar. Res. 6* : 74-83.

TONOLLI, V., 1949: Struttura Spaziale del Popolamento Mesoplanctico. Eterogeneita delle Densità dei Popolamenti Orrizontali e sua Variazione in Funzione della Quota. *Mem. Ist. ital. Idrobiol. de Marchi. 5* : 191-298.

———, 1958: Richerche sulla Microstruttura di Distribuzione dello Zooplancton nel Lago Maggiore. *Mem. Ist. ital. Idrobiol. de Marchi 10* : 125-52.

WINSOR, C. P.; WALFORD, L. A., 1936: Sampling variation in the use of Plankton Nets. *J. Cons. int. Explor. Mer. 11* : 190-204

# SOME OBSERVATIONS ON NATURAL FLUCTUATIONS OF TROUT POPULATION NUMBERS

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***Summary***

Five years' observations on Brown Trout in two small streams have shown that the populations are not in a stable state. There are fluctuations in the survival rates, and variations in the population numbers, weight, and composition. It is suggested that cannibalism is a factor in determining survival rates.

In one of these small streams, the removal of a moderate eel population has had no measurable effect on the trout population.

## Introduction

The observations described in this paper were made to determine the extent of the natural fluctuation in numbers of a Brown Trout population. The streams used, the Doyleston Drain and the Hanmer Road Drain, are small man-made tributaries of Lake Ellesmere which is a large shallow lake with a low-water area of 40,000 acres.

The streams have resident populations of Brown Trout, and in addition mature Brown Trout from the lake run into them to spawn, but do not remain. These lake fish are larger than the resident fish. The resident populations are not exploited by anglers.

The sampling areas on the Doyleston Drain were initially five separate 200 yard sections spaced throughout the stream. Only one of the 200 yard sections proved to be satisfactory for long term observations, and the length sampled at this point was increased in 1955 to 600 yards and in 1956, 1957, and 1958 to 1,000 yards.

The 1954 Hanmer Road Drain sample was from a 200 yard section. All subsequent samples were from one 900 yard long section, which included the area sampled in 1954.

Five years' observations are presented.

The number of trout present in the sampling areas has been estimated, using an electric fishing machine (Burnet, 1959).

## The Doyleston Drain

### *The Stream*

So far as can be determined, the physical nature of the section of stream under observation has been similar from year to year. The width is 9 ft and the water depth varies between 3 and 12 in. It flows

east-south-east and is not shaded by trees. Cover for trout is in the form of overgrown and undercut banks. The lowest water levels, and the highest temperatures occurred in the summer of 1955-56.

There was no interference from weed cleaning operations.

### *Ova Deposition*

The bed of the stream comprises suitable spawning gravels. In three spawning seasons it was possible to count the number of redds formed. The section of stream was examined at monthly intervals, and the position and size of redds noted. On subsequent visits the old redds were identified, and new redds noted.

The redds were classified into three groups, large—over 6 ft wide, medium—under 6 ft and over 3 ft wide, and small—under 3 ft wide.

The number of redds counted is given in Table 1. It can be seen that there is not a great difference in the ova deposition in the years observed, particularly if the ova content of a redd is approximately proportional to its size.

TABLE 1.—Doyleston Drain. The Number of Redds per 1000 Yards.

| Size | 1954 | 1955 | 1956 |
|---|---|---|---|
| Large | 19 | 34 | 20 |
| Medium | 29 | 25 | 64 |
| Small | 22 | 5 | 13 |
| Total | 70 | 64 | 97 |

The ova are derived both from the resident spawners and from spawners which have run up from the lake.

The resident females spawn in their third year, so that in 1955, the year of maximum numbers of third year and older fish, the total number of mature resident females was approximately 15 weighing 6·5 Kg (see Table 2).

In this year it is estimated that there were 33 female lake fish in the section, weighing 38·7 Kg. This figure is based on one sample only and does not allow for those fish which had already returned to the lake, or those which came after the sampling date.

The ova production of the resident fish can be calculated from Allen's (1951) formula, to be 1,060 ova per female making a total of 16,000 ova. Similarly from Allen's formula the lake spawners (47 cm average length) would average 1,900 ova per female. (Allen did not examine fish of this size, but his formula fits closely data given by Hobbs (1948) on the average ova content of 50 Lake Ellesmere trout.)

On the basis of 1,900 ova per female the contribution by lake spawners is 63,000 ova. Therefore the resident fish contribute, at the most, one-fith of the total ova deposited.

Four medium-size redds were dug and the numbers of ova recovered were, 388, 566, 590, 1,301. (Average 711.) These figures indicate that the medium-size redd approximates to the average found by Hobbs (1940) of 793 ova per redd. Therefore in 1955, if it is assumed that the small redds contained half this number, and the large redds twice this number, then the estimated total ova deposition is 76,000 ova. These figures indicate the density of the ova deposition.

The important point for present purposes is that the ova deposition was much greater than it would have been if the resident population was dependent only upon its own reproductive resources.

### *The Trout Population*

The population estimates were made in the winter each year, and in some years in mid-summer also. The date of the winter sampling was determined by weather conditions, and there is thus some variation from year to year. For comparison, the data presented have been corrected to a mean date of 1 August.

The results, giving numbers, average length, and estimated weights of three groups, the 1st, 2nd, and 3rd year and older fish, are presented in Table 2 and Fig. 1. The 1954 data are for a 200 yard long sample section; the 1955 data are for 600 yards and the sections in the remaining years were 1,000 yard lengths. The 1954 and 1955 data are converted to a 1,000 yard basis, and are therefore less accurate than the other years.

The separation of the 1st and 2nd year classes from the remainder was done from the length frequency distribution.

In the first 3 years, the number of 1-year-old fish declined from 150 to 83 to 44. The number then jumped to 490 in 1957, and dropped to 214 in the last year. A strong year class appeared in the 2-year-old group in 1958. The 1954 2-year-old group was also a strong year class,

TABLE 2.—Doyleston Drain. The Number, Length, and Weight of Age Groups at 1 August.

| Year of Sampling | 1st year | | | 2nd year | | | 3rd year and older | | Total No. | Total Wt. (Kg) |
|---|---|---|---|---|---|---|---|---|---|---|
| | No. | Length (cm) | Wt. (Kg) | No. | Length (cm) | Wt. (Kg) | No. | Wt. | | |
| 1954 | 150 | 17·8 | 10·2 | 58 | 27·3 | 14·2 | 15 | 5·7 | 223 | 30·1 |
| 1955 | 83 | 16·9 | 4·8 | 28 | 26·8 | 6·5 | 30 | 12·9 | 141 | 24·2 |
| 1956 | 44 | 16·1 | 2·8 | 16 | 26·6 | 3·4 | 13 | 4·7 | 73 | 10·9 |
| 1957 | 490 | 14·5 | 18·0 | 17 | 25·7 | 3·5 | 6 | 2·7 | 513 | 24·2 |
| 1958 | 214 | 16·5 | 11·6 | 88 | 25·5 | 17·6 | 18 | 8·3 | 320 | 37·5 |

Wt. (in Kg) × 3·6 = lb/acre.

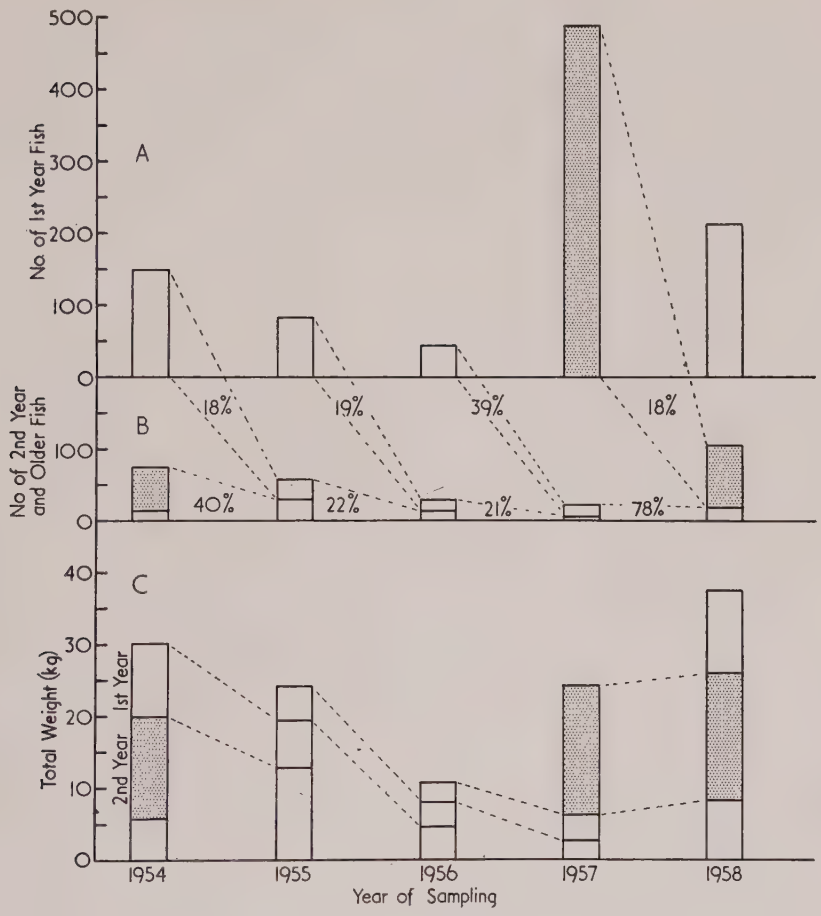


FIG. 1.—The Doyleston Drain population composition showing the strong year classes (stippled).
A. The number of 1st year fish.
B. The number of 2nd year (upper part of the bar) and the number of 3rd year and older fish (lower part of the bar)
C The population composition by weight The upper part of the bar represents 1st year fish, the mid part 2nd year fish, and the lower part 3rd year and older fish

which carried through to comprise most of the 3rd year and older group in 1955. The population, therefore, was dominated by the strong 1952 and 1956 year classes. Variations in the strength of the year classes cause fluctuations in the total number of fish, and the percentage age composition of the population. Therefore, the total weight changes, but not in proportion to the total number.

There was no restriction on the movement of trout in the stream, and it is probable that to some extent the results are affected by move-

ment into or out of the test sections. A significant movement down into the area by fingerlings or yearlings would have been detected, as the growth rate of the upstream fish was slower. The use of individual tags on the larger trout showed that they moved only short distances. There was no means of determining what numbers of fish emigrated to the lake but it is probable that a proportion of the "mortalities" were actually emigrations.

### *Growth Rate*

The average length of the 1- and 2-year-old groups at 1 August is shown in Table 2. It can be seen that the 1st year fish were smaller as well as more numerous in 1957.

The growth of fish between 20 and 30 cm in length can be compared over the periods, May to August 1956, and May to August 1957, when individually tagged fish were measured. The growth of 9 fish in 1956 was + 0·006 cm/day (Range — 0·001 to + 0·015), and of 10 fish in 1957 + 0·017 cm/day (Range + 0·002 to + 0·037), a significantly higher growth rate in 1957. These data indicate that the growth of the 0 + group does not influence that of the larger fish in this stream.

Comparisons between the growths shown for 2nd year fish in Table 2 are not made because it has been found (unpublished data) that growth rates determined from length frequency distributions do not necessarily represent actual growth as determined from individually tagged fish. The differences are due to differential mortality, or emigration.

A growth curve was constructed from the growth of individually tagged fish during 1956-57. The length was, 1-year-old (1 October) 17·8 cm, 2-year-old 27·0 cm, 3-year-old 32·5 cm, and 4-year-old 36·3 cm.

The largest resident fish captured was 39·2 cm, and there were few fish of over 36 cm. The population contains practically no fish of more than 4 years old.

### *Water Temperatures*

Maximum and minimum temperatures were recorded from 25/10/56 to 27/11/57. Readings were taken at approximately monthly intervals. The minimum temperature ranged from 4·4° C in late winter to 12·8° C in late summer. The maximum ranged between 10·6° C in mid winter and 28·3° C in late summer. The maximum temperature exceeded 20° C from at least the beginning of December to the end of February.

### *Eel Population*

The stream contains a moderate eel population. In 1954 the population density was estimated at 116 lb/acre, when 60% by number of the eels caught were *Anguilla australis* and 40% *Anguilla dieffenbachii*. The largest eel was 71 cm. There are therefore few eels of the size that prey on the larger trout (Burnet, 1952).

## THE HANMER ROAD DRAIN

### *The Stream*

This is a similar stream running parallel to the Doyleston Drain, one mile north of it, and flowing into Lake Ellesmere. There is a high bank and hedge (total height 10 to 12 ft) on the north side and the stream bed is shaded for part of the day. The stream also differs physically in that there are a series of weirs designed to limit the water velocity. There are pools immediately above and below the weirs. The stream bed contains a high proportion of sand.

The section of stream used in this test is 900 yards long by 11 ft wide with a weir at each end. The section contains two permanent pools formed by the weirs and a third pool formed by a bridge. The greater part of the section is shallow water with the margins overgrown by grasses and water weeds. There has been variation in the amount of this cover from year to year. It was at a minimum immediately prior to the 1956 and 1958 sampling as the stream had just been cleaned. The marginal cover was reduced drastically for one or two months.

### *Ova Deposition*

A successful redd count was made in 1955 when 12 large and 3 medium redds were counted. In 1957 14 female lake fish were counted in the section. Ova deposition is approximately one-third that of the Doyleston Drain. It is thought that the series of weirs has a deterrent effect on the migration of lake fish.

### *The Trout Population*

The population estimates were made in November each year, and in some years additional estimates were made throughout the year. From 1956 on, all fish caught were individually tagged, and age groups were determined from the tag data.

The results, giving numbers, average lengths, and total weights of the age groups are given in Table 3 and Fig. 2.

All data are for a 900 yard length of stream except the 1954 datum, which was derived from a 200 yard sample.

In the first 4 years the numbers of 1st year fish declined from 300 to 162, to 130, to 75 and then jumped to 244 in 1958.

The strong 1953 year class appeared as a strong 2nd year group in 1955. Again the effect of the strong year class was to alter the balance of the population, mainly by altering the proportion of 1st year and 2nd year fish.

The numbers of 3rd year and older fish remained fairly constant, increasing slightly in 1958.

A study of the tag data has shown that "survival" is in part immigration into the test section, and it has been demonstrated that "mortality" is in part emigration from the test area.

TABLE 3.—Hanmer Road Drain. The Number, Length, and Weight of Age Groups at 1st November.

| Year of Sampling | 1st year No. | 1st year Length (cm) | 1st year Wt. (Kg) | 2nd year No. | 2nd year Length (cm) | 2nd year Wt. (Kg) | 3rd year No. | 3rd year Length (cm) | 3rd year Wt. (Kg) | 4th year No. | 4th year Length (cm) | 4th year Wt. (Kg) | 5th year No. | 5th year Length (cm) | 5th year Wt. (Kg) | Total No. | Total Wt. (Kg.) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1954 | 300 | — | — | | | | | | | | | | | | | — | — |
| 1955 | 162 | 15·3 | 8·2 | 90 | 23·3 | 13·8 | ← | | | (22 | — | 9·1) | | → | | 274 | 31·1 |
| 1956 | 130 | 15·8 | 7·0 | 17 | 25·0 | 2·9 | 10 | 27·8 | 2·6 | 6 | 31·3 | 2·1 | 2 | — | 0·7 | 164 | 15·2 |
| 1957 | 75 | 17·5 | 6·1 | 26 | 23·6 | 4·6 | 10 | 27·5 | 2·5 | 5 | 31·6 | 1·8 | 1 | — | 0·6 | 118 | 15·7 |
| 1958 | 244 | 15·6 | 11·8 | 17 | 24·7 | 3·4 | 21 | 28·5 | 5·4 | 5 | 31·5 | 1·7 | 3 | — | 1·0 | 290 | 23·3 |

Wt. (in Kg) × 3·2 = lb/acre.

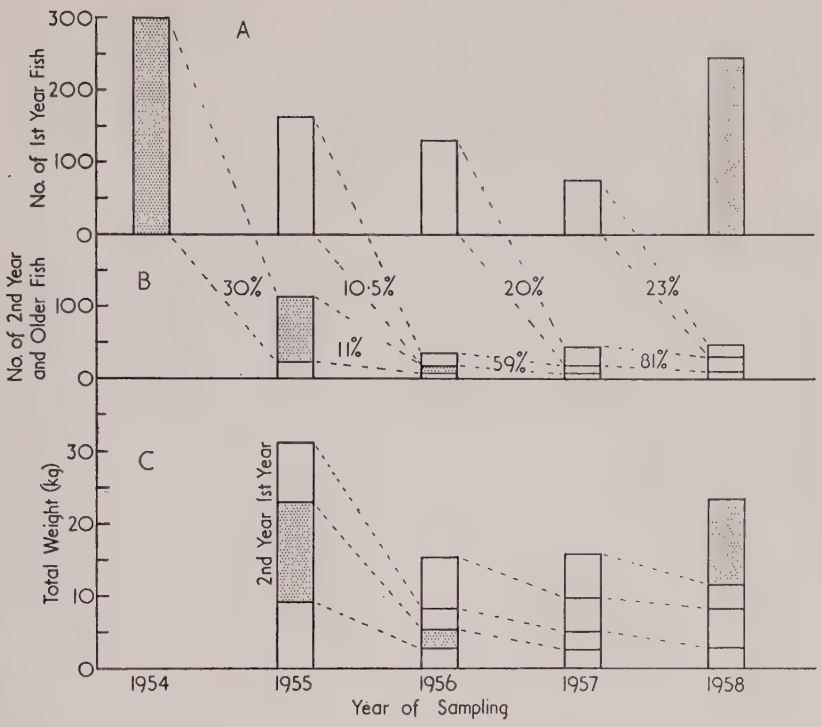


FIG. 2.—The Hanmer Road Drain population composition showing the strong year classes (stippled).

A. The number of 1st year fish.

B. The number of 2nd year fish (upper part of the bar), the number of 3rd year fish (mid part of the bar), and the number of 4th year and older fish.

C. The population composition by weight.

### *Growth Rate*

There is a negative correlation between the total weight of 1st year fish in the population and their growth rate. Similarly there appears to be a negative correlation between the growth of the 2nd year fish and the weight of 2nd year and older fish.

The average growth rate was 1 year old (1st October) 14·5 cm, 2 year old 22·9 cm, 3 year old 27·9 cm, 4 year old 31·2 cm, 5 year old 32·3 cm.

### *Water Temperatures*

The temperatures recorded on a maximum and minimum thermometer were very similar to the Doyleston Drain temperatures.

### *The Eel Population*

The eel population of this section of stream was removed in September 1956. The total of 18·4 Kg of eels (59 lb/acre) comprised 64% by number *Anguilla australis* and 36% *Anguilla dieffenbachii*. The largest eel was 70 cm. The section was kept free of eels for the remainder of the observation period.

## Discussion

It is obvious that neither population is in a stable state. Both show an interesting fluctuation in the numbers of 1st year fish. The patterns are similar, but in the Doyleston Drain the fluctuation is greater, and the peak occurred one year earlier. These fluctuations occur despite an ova deposition which is greater, and more constant than would be the case if the populations were entirely dependent upon their own reproductive resources.

It is possible that the fluctuations are initiated by some external factor, the existence of which has not been observed. The fact that the two cycles are out of step by one year suggests that the factor is not climatic. It is considered that the explanation lies within the trout population itself. Smith (1956), demonstrated at Crecy Lake that the survival of fingerlings to yearlings can be increased by reducing the number of larger fish present. Miller and Thomas (1952) obtained a lower survival of fingerlings as a lake population of larger fish increased. White (1924, 1927, and 1929) showed a relation between the survival of fry and the presence of older trout in a stream. Nicholls (1958) concluded that the survival of young trout is lower when there are older fish in the river.

From a study in progress on the South Branch, Waimakariri River, the author has found that there, in the absence of older trout, similar numbers of yearlings survive from 10 small + 3 medium redds, which is a much better survival than in the Doyleston Drain. The fluctuations observed may be a form of compensatory mortality, a result of either predation by older trout on the young, or possibly emigration caused by competition for space. The data presented show a 4-year cycle, which differs in form from the theoretical compensatory mortality cycles of Ricker (1954).

In the Doyleston Drain the survival rate is too low to prevent a decline in population numbers in 3 out of 4 years. The high numbers of the 1956 year class surviving to 1 year and 2 year old in 1957 and 1958, respectively, suggest that in the other years there is a surplus of cover available for fish of these sizes. Cover is only a possible limiting factor in only 1 out of the 4 years.

The Hanmer Road Drain population fluctuations are not so great. In general the survival rate increases with age, but there are marked variations from year to year. There is, for example, a poor survival of the 1953 year class from 2nd to 3rd year (11%). The presence of large numbers of the 1953 year class in 1955 has probably influenced

the 1st to 2nd year survival of the 1954 year class. It is considered that the explanation of the varying survival rates lies in the predatory relationship between trout of different sizes.

The Doyleston Drain is a special case in that all size groups of fish occupy the same cover, namely overgrown and undercut banks. One aspect of trout population dynamics is thus emphasised. In practice, there are varying degrees of separation of the different sizes of fish, depending upon the extent to which there is shallow water for the small fish, and deep water for the large fish. Population fluctuations of the Doyleston Drain type will be less marked as the physical separation of the large and small fish in a water increases. As the Hanmer Road Drain has some separation of sizes, the fluctuations are less marked.

The different growth rates affect the population structure. Length frequency distributions, based on the totals of 4 years, are shown in Fig. 3. It can be seen that the two curves are very similar, diverging only above 31 cm, and approaching zero at different sizes. It is significant that the curves are similar, despite differences in growth rate, and it appears that the slower growth rate is to some extent compensated for by a higher survival rate.

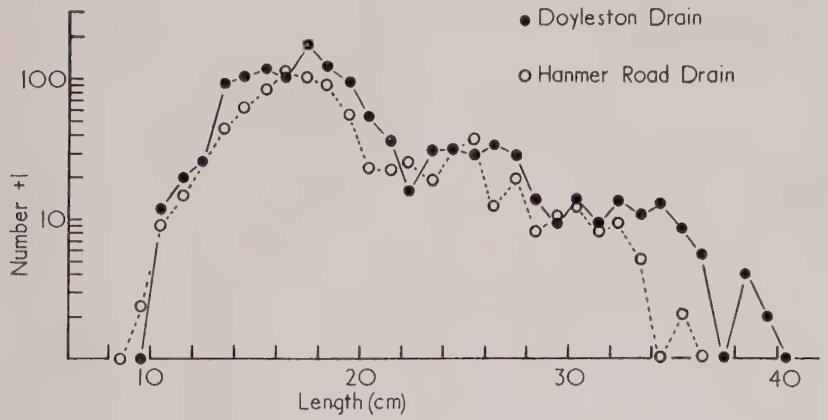


FIG. 3.—The length frequency distributions of the two populations.

The streams appear to offer little cover suitable for trout of over 35 cm in length. The behaviour of the lake fish, which run into these streams to spawn, indicates this. The lake fish were, in 1954, 45·6 cm average length, and 95% of them were between 35·5 cm and 55·0 cm. It is evident from the length frequency distribution that these fish do not remain in the streams after spawning. The maximum sizes observed relates to the maximum sizes approached by the growth curves. It may be coincidence that there is no cover for larger fish, or it is possible that the form of the growth curve is related to the size of the stream and is a space effect such as is described by Comfort (1956).

An eel population, slightly greater in weight than the trout population, was removed from the Hanmer Road Drain test section just prior to the 1956 sampling. So far as can be determined, there has been no major change in the survival rates. There has been some increase in the weight of trout and the numbers, but it appears that the changes are leading to a repetition of the 1955 state of the population.

## Conclusions

That trout have a high reproduction potential, the effectiveness of which is limited by cannibalism, is a hypothesis of practical importance. For example, in a stream where there is natural spawning in suitable gravel, and cover does not appear to be limiting the numbers of larger trout, attempts to increase the population by the addition of ova, fry or fingerlings, are not likely to produce a significant result. The data indicates that, in the same case, it would be possible to increase the numbers of larger fish by the introduction of a suitable large fish, but this would reduce recruitment from natural reproduction. It also shows that a trout population is plastic and capable of responding to increased exploitation. Higher mortality rates of the older fish (due to cropping) will be compensated in part by increased survival rates of the younger fish.

In small streams, where the eel population density is similar to the trout population density, and there are no very large eels, there is no evidence that the eel population affects the survival rates in the trout population. The absence of eels does not lead to greatly increased numbers of small trout, with a consequent reduction in the growth rate.

### *Management*

The data suggest a system of artificial stocking for those waters, usually lakes, where there is no natural reproduction and no protection for the small fish. Stocking with trout fry at intervals of 4 years would give the greatest return for the least effort. Thus, restocking should be delayed until natural mortality and cropping has reduced the population of older trout to a level where the fry released in the water have a good chance of survival. By keeping the population mainly to a single year class, the effects of cannibalism are reduced to a minimum. In unexploited, or lightly exploited populations, this cycle takes approximately 4 years, but it may be less in heavily exploited populations. Unpublished data on a lake population of Rainbow trout show that the same conclusions apply to this species.

This spaced system of stocking would present to the angler a population fluctuating in numbers and in size. Some natural populations behave in this way and there is no reason to believe that an artificially maintained population of this type should not be successful and acceptable to the angler.

ACKNOWLEDGEMENTS

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REFERENCES

ALLEN, K. R., 1951: The Horokiwi Stream: a study of a trout population. *Fish. Bull. Wellington, N.Z., 10* : 238 pp.

BURNET, A. M. R., 1952: Studies on the Ecology of the New Zealand long-finned Eel *Anguilla dieffenbachii* Gray. *Aust. J. Mar. Freshw. Res. 3* : 32-63.

———, 1959: Electric Fishing with Pulsatory Direct Current. *N.Z. J. Sci. 2* : 46-56.

COMFORT, A., 1956: "The Biology of Senescence". 257 pp. Routledge and Kegan Paul. London.

HOBBS, D. F., 1940: Natural Reproduction of Trout in New Zealand. *Fish. Bull. Wellington, N.Z., 8* : 93 pp.

———, 1948: Trout Fisheries in New Zealand; Their Development and Management. *Fish. Bull. Wellington, N.Z., 9* : 175 pp.

MILLER, R. B.; THOMAS, R. C., 1956: Alberta's "Pothole" Trout Fisheries. *Tran. Amer. Fish. Soc., 86* : 216-8.

NICHOLLS, A. G., 1958: The Population of a Trout Stream and the Survival of Released Fish. *Aust. J. Mar. Freshw. Res. 9* : 319-50.

RICKER, W. E., 1954: Effects of Compensatory Mortality upon Population Abundance. *J. Wildlife. Mgmt. 18* : 45-51.

SMITH, M. W., 1956: Further improvements in Trout Angling at Crecy Lake, New Brunswick, with Predator Control extended to Large Trout. *Canad. Fish. Culturist. 19* : 13-16.

WHITE, H. C., 1924: A Quantitative Determination of the Number of Survivors from Planting 5,000 Trout Fry in Each of Two Streams. *Contr. Canad. Biol. n.s. 2* : (No. 9) 137-49.

———, 1927: A Preliminary Report on Trout Investigation in Forbes Brook in 1925 and 1926. *Contr. Canad. Biol. Fish. n.s. 3* : (No. 15) 365-76.

———, 1930: Trout Fry Planting Experiments in Forbes Brook P.E.I., in 1928. *Contr. Canad. Biol. Fish. n.s. 5* : (No. 8) 203-12.

# THE THERMODYNAMIC STABILITY OF IRON AND ITS COMPOUNDS IN HYDROTHERMAL MEDIA

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## *Summary*

Phase diagrams for compounds of iron have been calculated over the temperature range 60° to 350° C from thermodynamic data, for saturated liquid water containing $H_2S$, $H_2$, and $CO_2$. The solid substances considered comprise pure Fe, FeS, $FeS_2$, $Fe_3O_4$, $Fe_2O_3$, and $FeCO_3$. The effect of the variables (gas contents and temperature) is discussed in relation to hydrothermal alteration and corroson caused by the fluids now being discharged at Wairakei.

It is shown that under present conditions, either $Fe_3O_4$ or $FeS_2$ could be the stable phase above 220° C. Low temperature, high $H_2S$ and low $H_2$ favour the stability of $FeS_2$. $FeS_2$ would, in general, be the final corrosion product of iron in hydrothermal media, their utilization for power being at temperatures lower than 220° C. FeS and $Fe_3O_4$ are possible corrosion intermediates and would be expected to lead to differing corrosion rates.

It is pointed out that the published figure for the standard free energy of formation of $Fe(OH)_2$ is based on a false assumption.


## INTRODUCTION

In relation to current investigations of hydrothermal fields and their utilization as a power source, the stability of iron compounds in this enviroment is important from two aspects.

### *Corrosion*

Iron, the basis of engineering construction, is thermodynamically unstable in water, and corrosion rates of its alloys are therefore of primary interest. Corrosion can be governed to a great extent by the physical and chemical characteristics of the corrosion product, e.g. the protective oxide film on aluminium.

A knowledge of the relative stabilities of the different compounds of iron that could contribute to the corrosion product is therefore of importance in considering inter-relations of corrosion rates determined experimentally under different conditions.

### *Geophysics and Petrology*

The results of petrological investigations on drilling cores obtained from the Wairakei field have shown the hydrothermal alteration of $Fe_3O_4$ to $FeS_2$. (Steiner, 1953.) This information was used initially to interpret magnetic surveys of the area, such that areas of low magnetic intensity indicated the alteration of $Fe_3O_4$ to $FeS_2$ and therefore indi-

cated the presence of hot water at depth. Later work included the magnetic examination of drill cores. (Studt, 1959.) In most cases, low values of magnetic polarization were obtained. In a few cases, higher values were obtained both where the sampling temperature was known to be low, and where the sampling temperature was known to be high. This would seem to indicate that $Fe_3O_4$ and $FeS_2$ were not far removed from equilibrium with each other under the naturally-occurring conditions.

A determination of the thermal and chemical conditions controlling the $Fe_3O_4/FeS_2$ equilibrium would be expected to throw further light on the method of magnetic prospecting.

The stability limits of other compounds could be of value in permitting deductions to be made with regard to the physical and chemical conditions existing at those points where they occur.

### *Substances Considered in Equilibrium Calculations*

The gas content of the geothermal bore discharges comprises approximately 0·02 mole % of the total discharge. Approximately 90 mole % of the gas is $CO_2$, the only other gases of importance being $H_2S$ (5 mole % and $H_2$ (1 mole %) (Wilson, 1955). These three were the only gases considered in calculating equilibria.

Water was considered only in the saturated liquid form. It is not envisaged that steam will be superheated more than a few degrees at any stage of the utilization, and then only in specific locations.

The solid phases considered comprise Fe, $Fe_3O_4$, $Fe_2O_3$, FeS, $FeS_2$, and $FeCO_3$. The formulae FeS and $FeS_2$ have been adopted in this paper because they were the formulae ascribed to the thermodynamic data used in the calculations. Other forms of iron sulphide (for which thermodynamic data are not available) and their structure have been discussed elsewhere. (Kullerud and Yoder, 1957; Meyer *et al.*, 1958.) Thermodynamic data for $Fe(OH)_2$ are not available for temperatures other than 25° C. The omission of these substances from the calculations is considered later.

### *Thermodynamic Data*

Heat content and entropy data for liquid water above 100° C were taken from steam tables. (Keenan and Keyes, 1936.) Thermodynamic data for liquid water below 100° C and for all other substances were obtained from Rossini *et al.* (1952), and Kelly (1949).

### *Calculation of Phase Diagrams*

Phase boundaries were obtained by following the equilibria between appropriate pairs of pure solid phases. It was assumed that no mixed phases are formed.

The substances considered in this study require that the equilibria of five reactions be calculated over the required temperature range. Those selected were:

$$3Fe + 4H_2O = Fe_3O_4 + 4H_2$$
$$Fe + H_2S = FeS + H_2$$
$$FeS + H_2S = FeS_2 + H_2$$
$$3Fe_2O_3 + H_2 = 2Fe_3O_4 + H_2O$$
$$FeS + CO_2 + H_2O = FeCO_3 + H_2S$$

Log $k_p$ as a function of temperature for each of these reactions was calculated by standard methods (Kubaschewski and Evans, 1955) from the published values of free energies of formation, heat contents, entropies, and heat capacities of the reactants. Log $k_p$ of the equilibrium between any other pair of solid phases was obtained algebraically from this information. For each equilibrium, log $k_p$ was then plotted as ordinate against reciprocal absolute temperature. (This gives an approximately linear curve.) As the calculations included water as the saturated liquid, the equilibrium constants were a function of the partial pressures of $CO_2$, $H_2S$, and $H_2$ ($p_{CO_2}$, $p_{H_2S}$ and $p_{H_2}$). Thus, for constant values of $p_{H_2S}$ and $p_{CO_2}$, the ordinate could be recalibrated for each reaction to read the equilibrium value of log $p_{H_2}$.

Log $p_{H_2}$ versus reciprocal absolute temperature for each reaction was then plotted on one diagram. Each line was marked to show on which side of it each solid phase participating in the reaction was stable. Areas of stability for each phase were readily deduced giving a phase diagram for given values of $p_{H_2S}$ and $p_{CO_2}$.

## RESULTS

Phase diagrams were required to cover the range of $p_{CO_2}$ and $p_{H_2S}$ encountered in saturated water at Wairakei, and for temperatures from 60° to 350° C. Conversion of the total discharge analyses of bores to partial pressures over saturated water at 250° C yields average values of 1, 0·03, and 0·05 atm. for $p_{CO_2}$, $p_{H_2S}$, and $p_{H_2}$ respectively.

Analyses at any time can lead to values differing from these averages by a factor of about 2 for $p_{CO_2}$, and by a factor of about 4 for $p_{H_2S}$ and $p_{H_2}$, due to possible variations in the total gas content by a factor of about 2, and possible variations in the proportion of $H_2S$ and $H_2$ in the gas by a factor of about 2.

The effect of lower values of $p_{CO_2}$ and $p_{H_2S}$ was required with regard to the nature of corrosion products of iron in media at lower temperatures and pressures. Reduction in the pressure of saturated liquid water causes the formation of a steam phase when exsolution of the gases and a reduction in their partial pressures would be expected.

The types of diagram obtained, and the effects of $p_{H_2S}$ and $p_{CO_2}$ as separate variables are shown in Figs 1-3.

## DISCUSSION

The effect on the phase diagrams of uncertainties in the thermodynamic data has not been estimated, because of the rather large naturally-occurring variations in the gas content of the bore discharges. Only qualitative deductions can be made from the effect of variables on the diagrams in so far as they effect their application to problems.

The omission of compounds for which thermodynamic data are not available must now be discussed.

Data for $Fe(OH)_2$ is available only for 25° C. Treatment of its equilibrium with Fe and $Fe_3O_4$ in the same way as the phase diagrams were determined, shows that $Fe(OH)_2$ has no range of hydrogen pressures over which it is stable at 25° C. This result is surprising in view of the stability of pure $Fe(OH)_2$ at 25° C (Linnenbom, 1958), and up to 100° C (Shipko and Douglas, 1956). However, consideration of the reactions involved and their standard free energy changes shows that the standard free energy of formation of $Fe(OH)_2$ need be only 1·7 kcal more negative for $Fe(OH)_2$ to be stable at 25° C. The figure given by Rossini *et al.* (1952) is based on the electrochemical results of Randall and Frandsen (1932a, 1932b). These workers used only one electrolyte concentration in their cells so no check of the reversibility of their cells can be made. However, the results obtained by Hampton (1926) for the cell

$$Fe(s),\ FeCl_2\ xM,\ HgCl(s),\ Hg(l)$$

over a range of concentration, combined with activity data for $FeCl_2$ given by Randall and Frandsen (1932b) permit a plot to be made of E, the potential of this cell, versus log mγ. The resulting straight line has a slope of 0·08 V instead of the slope of 0·029 V required by the postulated cell reaction:

$$Fe(s) + 2\,HgCl(s) = Fe^{++} + 2\,Cl^- + 2\,Hg(l)$$

The thermodynamic reversibility of Hampton's $Fe/Fe^{++}$ electrode is thus seriously in doubt. The agreement between the results of Randall and Frandsen (1932b) and Hampton (1926) means that the published figure for the standard free energy of formation is based on the false application of the reversible cell equation $\Delta G = -nEF$. The published figure is therefore useless.

The experimental investigations of the stability of $Fe(OH)_2$ referred to, suggest that the standard free energy of formation is in fact more highly negative than the published value. Evaluation of this point is required because of the importance of $Fe(OH)_2$ as a corrosion product intermediate (Gould and Evans, 1947; Douglas, 1957). Another effect which could affect the free energy is the contribution of surface energy in particles of very small size. This has been shown to affect the free energy of hydration of MgO to $Mg(OH)_2$ by 1·1 kcal. (MacDonald, 1955.)

The instability of pure $Fe(OH)_2$ above 100° C (Shipko and Douglas, 1956) ensures its absence from the phase diagrams above that temperature, while below 100° C, it is probably unstable with respect to iron sulphide, and so can be ignored in the present work.

While $Fe_9S_8$ has been shown to be an important intermediate in determining corrosion rates in $H_2S$-saturated air-free water at ambient temperatures (Meyer *et al.*, 1958) its temperature stability limit is not known. It was not detected by Rosenqvist (1954) in his thermodynamic study of sulphides at 500° C and above. No thermodynamic data are available for this compound, so it could not be included in the calculations. If it were stable above 60° C, it would be expected at hydrogen pressures higher than those of FeS, and it would, therefore, be less likely to occur naturally than FeS. (See later.) It may be an important corrosion intermediate at temperatures within the range of interest.

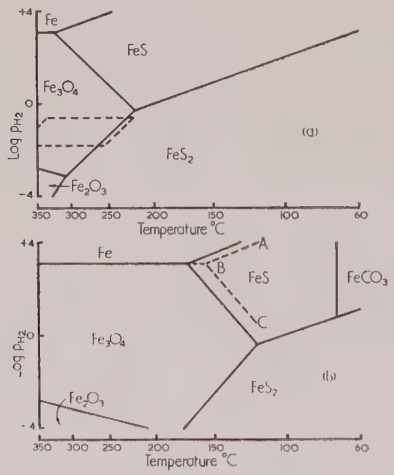


FIG. 1.

(a) $p_{CO_2} = 1$ atm., $p_{H_2S} = 10^{-2}$ atm.

(b) $p_{CO_2} = 1$ atm., $p_{H_2S} = 10^{-4}$ atm.

Rosenqvist (1954) has shown that the equilibrium ratio of $p_{H_2S}/p_{H_2}$ for FeS varies considerably over its non-stoichiometric range of composition. Extrapolation of his results to temperatures below 350° C gives good agreement with the present Fe/FeS equilibrium and qualitative agreement with the $FeS/FeS_2$ equilibrium. In the latter case, Rosenqvist's results give an equilibrium line at higher values of $p_{H_2}$ than that calculated. However, the extrapolation is not sufficiently valid to warrant any quantitative comparisons.

In general, the phase diagrams are considered sufficiently accurate to justify the following largely qualitative conclusions drawn from them.

Figures 1 (a) and (b) show the general form of the diagram, and, in combination, the effect of decreasing $p_{H_2S}$. The equilibria affected by $p_{H_2S}$ are moved in the direction of lower temperature. The equilibria $Fe/Fe_3O_4$ and $Fe_3O_4/Fe_2O_3$ are independent of $p_{H_2S}$ and therefore the triple points $Fe/FeS/Fe_3O_4$ and $Fe_3O_4/Fe_2O_3/FeS_2$ move along the lines representing these equilibria respectively.

The equilibrium constant for the reaction between FeS and $FeCO_3$ is $p_{H_2S}/p_{CO_2}$. This equilibrium is independent of hydrogen pressure and is therefore represented by a straight line parallel to the ordinate on

the type of phase diagram described. The position of this line is determined by the equilibrium temperature for the value of $p_{H_2S}/p_{CO_2}$ being considered. The plot of this log $k_p$ versus reciprocal absolute temperature gave a line of only very small positive slope with a value of $k_p$ of approximately $10^{-4}$. Thus, only a small decrease is required in $k_p$ at a value of about $10^{-4}$ for FeS to become unstable with respect to $FeCO_3$ over the whole temperature range. The effect of decreasing $p_{H_2S}$ over this range is illustrated in Figs 1(b) and 2.

Figure 1(b) shows the $FeS/FeCO_3$ equilibrium with $FeCO_3$ starting to appear at low temperatures. The equilibria (metastable under the conditions for which the diagram was determined) combining to fix the $Fe/FeCO_3/Fe_3O_4$ triple point are shown as dashed lines in Fig. 1(b). (AB = $Fe/FeCO_3$ equilibrium; BC = $Fe_3O_4/FeCO_3$ equilibrium). These equilibria are independent of $p_{H_2S}$ and are therefore fixed if $p_{CO_2}$ is fixed. When $p_{H_2S}$ is lowered from $10^{-4}$ to $10^{-4\cdot4}$ (approximately) the two triple points $Fe/Fe_3O_4/FeS$, $Fe/Fe_3O_4/FeCO_3$ coincide, while the $FeS/FeCO_3$ equilibrium moves rapidly in the direction of higher temperature such that FeS is no longer stable. The FeS phase is thus rapidly extinguished and a diagram of the type of Fig. 2 ($p_{H_2S} = 10^{-5}$) is obtained. Further reduction in $p_{H_2S}$ now affects only the $Fe_3O_4/FeS_2$, $FeCO_3/FeS_2$, and $Fe_2O_3/FeS_2$ equilibria leading to reduction in the $FeS_2$ area and increase in the $Fe_3O_4$ and $FeCO_3$ areas, as shown by the dashed lines for $p_{H_2S} = 10^{-6}$.

The effect of lowering $p_{CO_2}$ is shown by comparison of Figs 2 and 3.

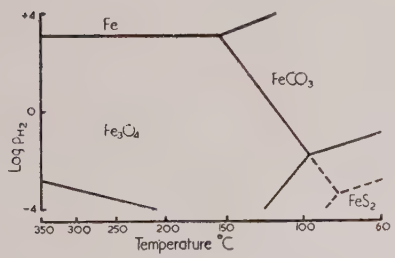


FIG. 2.—Full lines $p_{CO_2} = 1$ atm., $p_{H_2S} = 10^{-5}$ atm. Broken lines $p_{CO_2} = 1$ atm., $p_{H_2S} = 10^{-6}$ atm.

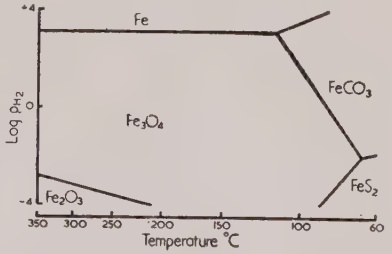


FIG. 3.—$p_{CO_2} = 10^{-1}$ atm., $p_{H_2S} = 10^{-6}$ atm.

The triple point $Fe/Fe_3O_4/FeCO_3$ is moved from 155° C to 115° C for a decrease in $p_{CO_2}$ from 1 to 0·1 atm.

Since $p_{H_2S}/p_{CO_2}$ is approximately $10^{-2}$ in saturated geothermal water.

and since exsolution of the gases when a steam phase is formed does not change this ratio significantly, $FeCO_3$ would not be expected, in general, to occur as a mineral, at Wairakei.

Its occurrence in Bore 6 in the Wairakei field (Steiner, 1953) can be accounted for by the reduction in the $H_2S$ content in this part of the field. (Wilson, 1955.)

Consequent on the exclusion of $FeCO_3$ and its reactions from consideration, the application of the range of $p_{H_2}$ encountered in the field to the diagrams shows that the $Fe_3O_4/FeS_2$ equilibrium is the only one likely to be important geologically.

Figures 1(a) and 1(b) show that the lowest value of $p_{H_2}$ for which FeS is stable is that at the triple point $Fe_3O_4/FeS/FeS_2$, and that this does not vary significantly with change in $p_{H_2S}$. Thus, for FeS to occur as a stable phase, $p_{H_2} > 0{\cdot}5$ is required. The highest recorded value of $p_{H_2} = 0{\cdot}24$, so that the natural occurrence of FeS is unlikely in material in equilibrium with the present hydrothermal fluid.

It has been shown how variations in $p_{H_2S}$ affect the $Fe_3O_4/FeS_2$ equilibrium. Its two extremes of position as determined by the natural variations in $p_{H_2S}$ are shown as broken lines in Fig. 1(a) bounded by the limits of variation of $p_{H_2}$. Projection of the resulting parallelogram on the temperature axis gives the temperature range between which it is possible for $Fe_3O_4$ and $FeS_2$ to be in equilibrium under the various naturally occurring conditions. Thus, it is not possible to say, in general, whether $Fe_3O_4$ would react to form $FeS_2$, or vice-versa, in saturated geothermal water at temperatures above 220° C.

It must be stressed that these arguments apply to reactions of the compounds under the *present* Wairakei conditions.

The gas contents obtained by analysis of fluids from bores which have been discharging for up to 6 years are by no means necessarily the same as those obtaining when the hydrothermal alteration, currently being detected petrologically, took place. Further, it is not possible to say when the alteration occurred or how rapidly alteration would be expected to proceed. The detection of a compound in a drill core may mean that that compound was the stable phase when the hole was drilled. However, if alteration rates are slow, the compound may not necessarily be stable in the fluid sampled at the completion of drilling. The detection of $Fe_3O_4$ magnetically indicates only that, at some time previous to drilling, a suitable combination of temperature, $p_{H_2S}$ and $p_{H_2}$ existed to make $Fe_3O_4$ stable. The previous discussion shows that low temperature, low $p_{H_2}$, and high $p_{H_2S}$ favour FeS.

In the application of phase diagrams to corrosion it must be remembered that corrosion is not an equilibrium process. However, the dia-

grams can be used to indicate possible corrosion products. The phase diagrams, gas solubilities, and the thermodynamics of water/steam equilibria show that, in general, $FeS_2$ would be the stable form (i.e. the final corrosion products) of iron in the range of media likely to be encountered in the exploitation of geothermal power. During the formation of $FeS_2$ fom Fe, compounds intermediate in stability would be expected. For example, Fe forms successive layers of FeO, $Fe_3O_4$ and $Fe_2O_3$ on scaling in oxygen at high temperatures (Davies *et al.*, 1951), and successive layers of $Fe_9S_8$, FeS, and $FeS_2$ on corroding in water at ambient temperatures with $p_{H_2S} = 1$ atm. (Meyer *et al.*, 1958). The phase diagrams show that both $Fe_3O_4$ and FeS should be considered as possible intermediates in the hydrothermal media. The diffusion rates of the reacting species through the corrosion product (Himmel *et al.*, 1953), and the electrical properties of the corrosion product (Hoar and Price, 1938) are known to be important factors in influencing reaction rates. $Fe_3O_4$ and FeS would be expected to show quite different behaviour in these respects, and their presence in different amounts in the corrosion product should therefore lead to different corrosion rates. Accordingly experiments are being conducted to determine the types of corrosion products obtained in different hydrothermal media, and to correlate the types of corrosion products with the phase diagrams and measured corrosion rates. It is possible that in this way a knowledge of the factors determining corrosion rates will be obtained.

## ACKNOWLEDGEMENTS

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## REFERENCES

DAVIES, M. H.; SIMNAD, M. T.; BIRCHENALL, C. E., 1951: On the Mechanism and Kinetics of the Scaling of Iron. *J. Metals, N.Y. 3* : 889-96.

DOUGLAS, D. L., 1957: Fundamental Aspects of Iron Corrosion. *In* "Corrosion and Wear Handbook", McGraw-Hill Book Coy. Inc., New York: pp. 11-20.

GOULD, A. J.; EVANS, U. R., 1947: Some Experiments on Corrosion of Steel by Boiling Water. *J. Iron St. Inst. 155* : 195-200.

HAMPTON, W. H., 1926: The Potential of the Iron Electrode. *J. phys. Chem. 30* : 980-91.

HIMMEL, L.; MEHL, R. F.; BIRCHENALL, C. E., 1953: Self-diffusion of Iron and Iron Oxides and the Wagner Theory of Oxidation. *J. Metals, N.Y. 5* : 827-43.

HOAR, T. P.; PRICE, C. E., 1938: The Electrochemical Interpretation of Wagner's Theory of Tarnishing Reactions. *Trans. Faraday Soc. 34* : 867-74.

KEENAN, J. H.; KEYES, F. G., 1936. "The Thermodynamic Properties of Steam". Wiley and Sons, New York.

KELLEY, K. K., 1949: Contribution to the Data on Theoretical Metallurgy. X. High-temperature, Heat-content, Heat-capacity, and Entropy Data for Inorganic Compounds, *U.S. Bur. Min. Bull. 476.*

KUBASCHEWSKI, O.; EVANS, E. LL., 1955: "Metallurgical Thermochemistry". Pergamon Press, London; 2nd. Edit., pp. 4-32.

KULLERUD, G.; YODER, H. S., 1957: The Fe-S System. *Yearb. Carneg. Instn 56* : 187-91.

LINNENBOM, V. J., 1958: The Reaction between Iron and Water in the Absence of Oxygen. *J. electrochem. Soc. 105* : 322-4.

MACDONALD, G. J. F., 1955: The Gibbs Free Energy of Water at Elevated Temperatures and Pressures with Applications to the Brucite-Periclase Equilibrium *J. Geol. 63* : 244-52.

MEYER, F. H.; RIGGS, O. L.; MCGLASSON, R. L.; SUDBURY, J. D., 1958: Corrosion Products of Mild Steel in Hydrogen Sulphide Environments. *Corrosion 14* : 109t-15t.

RANDALL, M.; FRANDSEN, M., 1932a: Determination of the Free Energy of Ferrous Hydroxide from Measurements of Electromotive Force. *J. Amer. chem. Soc. 54* : 40-6.

————, 1932b: The Standard Electrode Potential of Iron and the Activity Coefficient of Ferrous Chloride. *J. Amer. chem. Soc. 54* : 47-54.

ROSENQVIST, T., 1954: A Thermodynamic Study of Iron, Cobalt, and Nickel Sulphides. *J. Iron St. Inst. 176* : 37-57.

ROSSINI, F. D.; WAGMAN, D. D.; EVANS, W. H.; LEVINE, S.; JAFFE, I., 1952: Selected Values of Chemical Thermodynamic Properties. *Nat. Bur. Stand. Circ. 500,* U.S. Government Printing Office, Washington.

SHIPKO, F. J.; DOUGLAS, D. L., 1956: The Stability of Ferrous Hydroxide Precipitates. *J. phys. Chem. 60* : 1519-23.

STEINER, A., 1953: Hydrothermal Rock Alteration at Wairakei, N.Z. *Econ. Geol. 48, 1* : 1-13.

STUDT, F. E. In press: Magnetic Survey of the Wairakei Hydrothermal Field. *N.Z. J. Geol. Geophys.*

WILSON, S. H., 1955: Chemical Investigations. *In* Geothermal Steam for Power in New Zealand. *N.Z. Dep. sci. industr. Res. Bull. 117* : pp. 27-42.

# THE POSSIBILITIES OF NATURAL RADIOCARBON AS A GROUND WATER TRACER IN THERMAL AREAS

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***Summary***

An evaluation of the factors that affect the $^{14}C$ concentration of the carbon dioxide coming to the surface with water and steam in the thermal areas, shows $^{14}C$ measurements can assist in the study of the underground movement of water.

Measurements so far carried out at five locations in the Wairakei thermal area of New Zealand show that the time for appreciable underground circulation of water in this area is less than 40,000 years for travel from the surface to depths of 1,500 ft or more.

## Introduction

Over the last few years studies of the distribution of $^{14}C$ in Nature have been carried out by many workers and $^{14}C$ has proved to be a useful tool for determining water movement in the ocean. On the other hand when the work reported here was undertaken, $^{14}C$ measurements had not been investigated for their value in studying water movement underground. Recently, Broecker and Walton (1959) have reported investigations of the $^{14}C$ concentration of surface water and Brinkmann *et al.* (1959) have, by $^{14}C$ data, measured the age of water from several water-supply wells in Germany.

One of the basic principles of the radiocarbon dating method (Libby, 1955) is that the major part of the $^{14}C$ on Earth is produced in the atmosphere by cosmic ray neutrons. The production of $^{14}C$ below the surface of the earth can only occur as a result of the small residual cosmic ray neutron flux that penetrates the atmosphere, and the relatively few neutrons from the spontaneous fission of traces of uranium present in all soils and rocks.

The resulting specific activity of underground carbon due to the $^{14}C$ produced in this way is negligibly small when compared to the $^{14}C$ specific activity of atmospheric carbon. It thus follows that no matter where on Earth $^{14}C$ is detected (with the current sensitivity limits of detection equipment) it must have come originally from the atmosphere. As $^{14}C$ is a radioactive isotope (half-life 5,570 years), its detection at any point on Earth shows that it has travelled from the atmosphere to that point in a time less than the maximum age limit of current radiocarbon dating equipment—approximately 50,000 years if several days counting are allowed for each sample measurement (Fergusson, 1955).

The tritium method of measuring the age of water samples (Kaufman and Libby, 1954) is now widely used. Although tritium (half-life 12·5 years), being an isotope of hydrogen, is theoretically ideal for this purpose, the maximum time range over which it can be used is in practice only 50 years. Samples of water from geothermal wells at Larderello, Italy, proved to be older than 50 years, as no tritium was detectable (Buttlar and Libby, 1955) and it is expected that a similar result will be obtained by tritium measurements on deep waters from New Zealand thermal areas. As water always contains some carbon dioxide in solution it would therefore be valuable if $^{14}C$ with its longer half-life of 5,570 years could be used to extend the time range over which the age of water can be determined.

In endeavouring to use the $^{14}C$ concentration of $CO_2$ as a tracer for water movement, allowance must be made for the possibility of relative movement of $CO_2$ and water, due to diffusion of $CO_2$ through the water. However, the diffusion of $CO_2$ through still water is a slow process. The $^{14}C$ content of ground water would be reduced to 0·1% of its initial value in the time taken to diffuse 150 ft. Thus, if $^{14}C$ is detected more than 150 ft underground, it almost certainly was carried down by actual movement of the water. The role of ground water in the Wairakei hydrothermal system has been considered in some detail by Studt (1957). For the Wairakei thermal area there is also available a considerable amount of data on the geology of the area, chemical analyses of waters and gases, temperature distribution, etc. (Grange, 1955). No attempt has been made in this paper to correlate all this data with the few $^{14}C$ measurements available to date, as the aim has been to evaluate the interaction of the main factors that have to be taken into account if $^{14}C$ measurements are used for the study of underground water movement. These factors are: the decay of $^{14}C$, the addition underground of $^{14}C$-free $CO_2$, the separation of $CO_2$ and $H_2O$, and the "young" $CO_2$ concentration in surface water. When further $^{14}C$ measurements are available, it may be possible to combine them with the other data and attempt an interpretation in terms of a detailed model of water movement.

## EXPERIMENTAL PROCEDURE

Essentially, the method involves collecting the sample (steam, water, and $CO_2$) in a flask containing $Ba(OH)_2$. The steam condenses and the $CO_2$ precipitates out as $BaCO_3$, this process continuing until the flask is full of water. Later the $CO_2$ is re-evolved, by treatment of the $BaCO_3$ with dilute HCl. The $^{14}C/^{12}C$ ratio of the sample is then measured by the radiocarbon dating equipment.

### *Collection of Sample*

The complete apparatus for the collection of carbon dioxide samples from bores is shown in Fig. 1. The condenser and cyclone water-steam separator are used solely to increase the $CO_2/H_2O$ ratio of the steam entering the collection flask, and thus may be omitted in some cases.

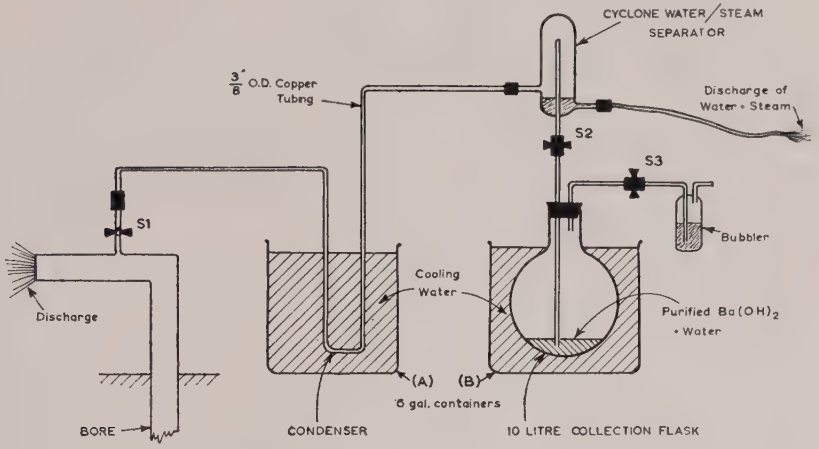


FIG. 1.—Apparatus for collection of $CO_2$ from geothermal bores.

At bore 13, where the discharge has a low $CO_2/H_2O$ ratio both the condenser and the separator were used, while at bore 30 only the separator was necessary. For collections from fumaroles neither the condenser nor the separator is necessary, the copper tube simply being pushed well down into the fumarole.

The collection is started without any cooling water in containers A and B. Stopcock $S_1$ is opened and steam is allowed to flow through the condenser and water-steam separator to flush out all the air. Stopcocks $S_2$ and $S_3$ are then opened so that steam flows through the collection flask and attached bubbler. After a few minutes the $Ba(OH)_2$ in the collection flask dissolves as the water is heated to boiling point and all air is swept out of the collection flask by the steam. The water in the bubbler will then commence boiling. Steam is allowed to sweep through the collection flask for a further 5 min. so that there is no possibility of any air remaining in the collection flask. Stopcock $S_3$ is then closed and cooling water added to container B. At this stage it may be necessary to increase the flow through $S_1$ so that air is not sucked back into the collection flask as a result of the increased rate of steam condensation. Cooling water may then be added to container A, the flow through $S_1$ being adjusted so as to maintain a small loss of steam along with the water from the cyclone separator. The efficiency of the condenser may be controlled by varying the length of the copper tube immersed in the cooling water.

After approximately 2 hr the flow of steam into the collection flask will cease. At this stage the flask is almost completely full of water—a few ml of gas non-absorbable by the $Ba(OH)_2$ solution being trapped in the neck of the flask. The collection flask is then disconnected and the $BaCO_3$ allowed to settle. The clear solution may then be sucked off and the $BaCO_3$, as a slurry, transferred to a smaller flask for transport to the laboratory.

*Preparation of Carbonate-free $Ba(OH)_2$*

In the first measurements of this series (1954-55) the preparation of carbonate-free $Ba(OH)_2$ solution was done by dissolving "Analar" $Ba(OH)_2$ in boiling water and then filtering off the hot $Ba(OH)_2$ solution. However, a trace of $BaCO_3$ is usually present in the filtrate, so in the latest measurements (1957), the $Ba(OH)_2$ used for the collection of the sample was prepared in the laboratory by the following method.

Two litres of $Ba(OH)_2$ solution, saturated at 100° C, was p in a 3-litre flask. Ten litres of $^{14}C$-free $CO_2$ (prepared by bur ) was then added to this solution so as to reduce the $^{14}C$ spe vity of the $BaCO_3$. (Some of the resulting $BaCO_3$ precipita as later analysed for $^{14}C$ content and was found to have a specific activity of 8% of that of atmospheric $CO_2$.) After the solution had boiled for a few minutes it was allowed to cool slowly to 80° C when the $Ba(OH)_2$ solution was withdrawn. Slow cooling of the solution allowed the $BaCO_3$ to settle, and as the solution cooled from 100° C to 80° C the $Ba(OH)_2$ that was precipitated carried down any traces of $BaCO_3$ suspended in the liquid.

*Possibility of $^{14}C$ Contamination of Sample*

As the $^{14}C/^{12}C$ ratio of the samples measured is low, of the order of 1% of atmospheric $^{14}C/^{12}C$ ratio, adequate precautions must be taken to guard against the contamination of the sample by appreciable amounts of $^{14}C$. There are two sources of such contamination—

(1) The $^{14}C$ in the $BaCO_3$ which occurs as an impurity even in analytical reagent grade $Ba(OH)_2$

(2) The $^{14}C$ in atmospheric $CO_2$.

Considering (1)—In a typical sample collection, e.g. bore 30, 15 litres of $CO_2$ was collected together with 10 litres of condensate in the collection flask, thus producing 134 g $BaCO_3$. As the $BaCO_3$ in the 3-litre flask used for preparing the purified $Ba(OH)_2$ had a $^{14}C$ specific activity of only 8% of atmospheric $CO_2$ (due to the introduction of $^{14}C$-free $CO_2$) the amount of this $BaCO_3$ needed to give an error equal to the probable assay error of 0·1% is

$$134 \times \frac{1}{1000} \times \frac{100}{8} = 1{\cdot}68 \text{ g } BaCO_3$$

The solubility of $BaCO_3$ in $Ba(OH)_2$ solution, saturated at 80° C (which contains approximately 70 g $Ba(OH)_2$ per 100 ml solution) is approximately $10^{-6}$ g per 100 ml solution, which is negligible. It thus appears that contamination of the $Ba(OH)_2$ with $^{14}C$ from the $BaCO_3$ cannot cause a detectable error in these measurements.

Considering (2)—Contamination by atmospheric $CO_2$ was avoided by carrying out all transfers of $Ba(OH)_2$, after it had been purified,

inside apparatus closed to the atmosphere and filled with air drawn through "Carbosorb". An error of 0·1% in the ratio of the $^{14}C$ content of the sample to that of atmospheric $CO_2$, caused by the addition of atmospheric $CO_2$ would require 15 ml of atmospheric $CO_2$ to be added to the sample in the above case where 15 litres of $CO_2$ were collected. As the $CO_2$ content of air is 0·03% by volume, 50 litres of air would be required to supply the 5 ml of $CO_2$. With the collection procedure used, such an amount of atmospheric contamination is highly improbable.

The consistent results obtained from those fumaroles in which measurements were repeated (Table 1) is further evidence that $^{14}C$ contamination was probably negligible in all measurements.

### *Selection of Sampling Locations*

The five steam discharges sampled to date are all in the Wairakei area. Two samples are from wells drilled in connection with the search for geothermal steam, while three are from fumaroles.

Bore 30 was chosen because it is a deep well situated almost in the middle of the best steam producing area. The basic characteristics of this well are: (Smith, 1958) drilled to 2238 ft, cased to 1505 ft, total mass discharge 630,000 lb per hour at approximately 260° C. It was

TABLE 1.—$^{14}C$ Content of Steam Discharges in the Wairakei Area.

| Location | Date Sampled | $^{14}C/^{12}C$ ratio as % of normal groundwater value | $CO_2/H_2O$ (moles $CO_2$ per $10^6$ moles $H_2O$) | $^{14}C/H_2O$ Equiv. "young" $CO_2/H_2O$ (moles $CO_2/10^6$ moles/$H_2O$ |
|---|---|---|---|---|
| Bore 30 | September 1957<br>September 1957 | $0·58 \pm 0·25$<br>$0·43 \pm 0·15$ } $0·50 \pm 0·1$ | 170 | $0·85 \pm 0·17$ |
| Bore 13 | September 1957 | $1·4 \pm 0·25$ | 17 | $0·24 \pm 0·05$ |
| Fumarole 712 (Karapiti) | December 1954<br>May 1955<br>September 1957 | $0·75 \pm 0·3$<br>$0·75 \pm 0·2$<br>$0·77 \pm 0·15$ } $0·75 \pm 0·1$ | 560 | $4·2 \pm 0·80$ |
| Fumarole 712A | May 1955 | $1·8 \pm 0·2$ | 120 | $2·2 \pm 0·25$ |
| Fumarole 612 | December 1954<br>May 1955 | $0·45 \pm 0·2$<br>$0·65 \pm 0·15$ } $0·55 \pm 0·1$ | 1610 | $8·9 \pm 1·6$ |
| Groundwater (average values) | — | 100 | 10<br>40 | 10<br>40 |
| Seawater | — | 100 | | |

therefore expected to be low in $^{14}C$ content. Bore 13, on the other hand is outside the main production area, and if it is in an area of recharge, its water would be expected to be higher in $^{14}C$ content than bore 30. The basic characteristics of this well are: drilled to 1402 ft, cased to 728 ft, total mass discharge 130,000 lb per hour at approximately 200° C.

Karapiti (fumarole 712) was chosen because it is the largest fumarole in the Wairakei area, discharging 35,000 lb of steam per hour at 114° C. It is also relatively close to bore 13. Fumarole 712A is a small vent which has only appeared in recent years. It was chosen because of its proximity to Karapiti—approximately 300 ft due east. Fumarole 612 lies on the opposite side of the main producing area from Karapiti, being at the head of Geyser Valley due north from the main producing area.

## RESULTS

The results of the measurements of $^{14}C/^{12}C$ ratio of the $CO_2$ from the above sources are given in Table 1. The $CO_2$ to $H_2O$ ratios for the fumaroles are derived from the measurements of the amount of $CO_2$ collected as $BaCO_3$ and the amount of condensed steam associated with this $CO_2$. The $CO_2$ to $H_2O$ ratios for the bores have been supplied by Mr S. H. Wilson, using the methods described by Wilson (1955). The errors indicated are the standard deviations due to counting only. For comparison purposes the values for seawater (Libby, 1955) and for average groundwater (Goldschmidtt, 1954) are also included.

## DISCUSSION

From measurements of the H/D and $^{16}O/^{18}O$ isotope ratios of thermal waters from many parts of the world, Craig *et al.* (1955) has shown that the water coming to the surface in thermal areas is mainly of groundwater origin, and that the magmatic water contribution is less than several per cent. Thus, the effect of magmatic water on the data presented here will be less than the other uncertainties involved so that it can be assumed that the emerging water is entirely of groundwater origin. The $^{14}C$ measurements give the $^{14}C/^{12}C$ ratio of the $CO_2$ in the sample and, as the $CO_2/H_2O$ ratio is known, the $^{14}C/H_2O$ ratio may be obtained. There are, however, five main factors that can affect the $^{14}C/^{12}C$ and $^{14}C/H_2O$ ratios of the sample $CO_2$ and $H_2O$. (The effects of isotopic fractionation on the data so far collected would be much less than the experimental error in the measurements of the $^{14}C/^{12}C$ ratio and so may be neglected.) These five factors will now be considered individually.

(1) Age—this reduces the $^{14}C/^{12}C$ ratio, depending on the time that has elapsed since the $CO_2$ in the sample ceased to be in exchange with the atmosphere. The $^{14}C/H_2O$ ratio is also reduced by the same percentage as the $^{14}C/^{12}C$ ratio.

(2) Dilution—the addition of "$^{14}C$-free" $CO_2$ as gas or carbonate ion to the $CO_2$, originally of atmospheric origin, in the underground water will reduce the $^{14}C/^{12}C$ ratio but the $^{14}C/H_2O$ ratio will not be altered.

(3) Concentrating Factor—separation of $CO_2$ and $H_2O$ with a consequent change in $CO_2/H_2O$ ratio can occur—(enrichment in one place coupled with depletion in another). This process does not change the $^{14}C/^{12}C$ ratio but does change the $^{14}C/H_2O$ ratio of the sample. The concentrating factor is defined as the ratio of the groundwater $CO_2$ concentration of the sample divided by the $CO_2$ concentration of the groundwater. Thus, if no separation occurs the concentrating factor has a value of one.

(4) Concentration of $CO_2$ in surface groundwater—the $CO_2$ is assumed to be in exchange with atmospheric $CO_2$, either directly, or indirectly through the biosphere. The relevant concentration is not necessarily the present value for surface water in the vicinity, but the value at some time in the past, when the present upwelling water left the surface—(maybe up to 40,000 years ago).

Minimum and maximum limits can be set for the value of the $CO_2$ concentration in surface groundwater that would apply for the Wairakei thermal area. The absolute minimum would be the value for rainwater, 0·3 mol. $CO_2/10^6$ mol. $H_2O$ (Hutchinson, 1954), and as most soils contain at least several times the rainwater concentration of $CO_2$ a more likely minimum value is 1 mol. $CO_2/10^6$ mol. $H_2O$. The maximum value found in New Zealand soils is 100 mol./$10^6$ mol. $H_2O$ (Mr H. R. Penhale, pers. comm.) and this only occurs in soils of high organic content. The Wairakei soils are generally rather low in organic content and therefore a more likely maximum value is 30 mol. $CO_2/10^6$ mol. $H_2O$. These minimum and maximum values are in agreement with the average value for $CO_2$ concentration of surface groundwater and rivers of 10 mol. $CO_2/10^6$ mol. $H_2O$. (Goldschmidtt, 1954).

(5) Exchange of carbon—the exchange of carbon between $CO_2$ in solution in the water and the carbonate material underground is a possibility that eventually must be considered. It may be possible to investigate such exchange and its effect on these data by determining the $^{14}C/^{12}C$ ratio of carbonate material from core samples. The possibility of this exchange of carbon has been neglected in the following discussion for two reasons: firstly, because its effect on $^{14}C$ content of the water would most likely be less than the other factors outlined (Brinkmann *et al.*, 1959), and secondly because, if present, its effect would be the same as a reduction in the concentration of $CO_2$ in surface groundwater or an increase in age.

In any actual situation, all of the above factors are probably influencing the observed ratios. The present available data does not allow complete separation of the effects of these factors, but their interdependence can be elucidated and is shown in Fig. 2.

In Fig. 2 the concentration of "young" $CO_2$ in the groundwater is plotted against the concentrating factor. For any given age of the sample there is a reciprocal relation between possible combinations of the young $CO_2$ concentration in the groundwater and the concentrating factor that will satisfy the observed $^{14}C/H_2O$ ratios. This relation when plotted on log-log paper appears as a straight line with a negative slope. The observed $^{14}C/^{12}C$ ratios fix maximum and minimum

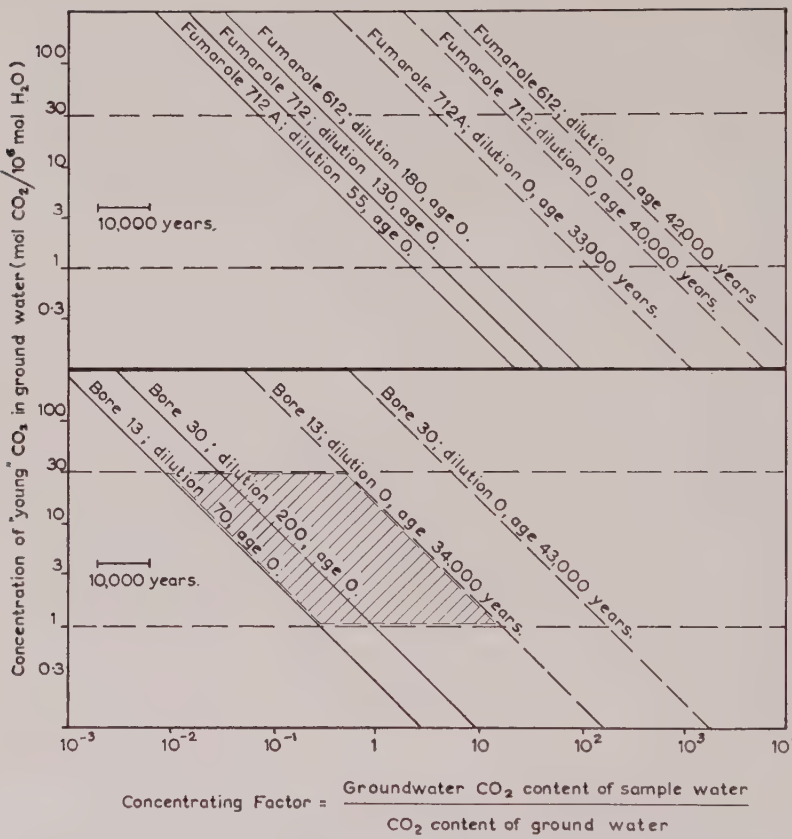


FIG. 2.—Diagrammatic representation of the interdependence of the various factors affecting the $^{14}C$ content of water from the geothermal areas.

values for both the age of the $CO_2$ carried down with the groundwater and the dilution with $^{14}C$-free $CO_2$—the maximum age corresponding to the minimum dilution and vice-versa. The extreme cases of zero age and of zero dilution are represented in Fig. 2 by the two appropriate lines for each bore and fumarole sampled. As the maximum and minimum values of the $CO_2$ concentration in groundwater are known, indicated by dotted horizontal lines in Fig. 2) the range of possible combinations of values of the various factors affecting $^{14}C$ concentration in the sample is definitely limited. Thus, permissible values of the time since the $CO_2$ left the surface, the fraction of old $CO_2$ added, the concentrating factor, and the concentration of young $CO_2$ in the groundwater for a given sample, correspond to points in Fig. 2 lying within a parallelogram defined by lines corresponding to the maximum and minimum limits of $CO_2$ concentration in groundwater, and the lines corresponding to zero and maximum age for the young $CO_2$ in the sample water. The appropriate parallelogram for

the case of bore 13 is shown shaded in Fig. 2. As further data on the above variables is obtained the area of the parallelogram in Fig. 2 will be reduced so that the age of the $CO_2$ and water will be confined within narrower limits. Further samples have been collected with the above aim in view.

### *Direction of Water Flow*

From the data on $^{14}C$ content of water of bore 13 and bore 30, some conclusions can be drawn regarding direction of movement of water and gas. It can be shown that very little, if any, of the $^{14}C$ emerging in bore 30 has come from the vicinity of bore 13, for, postulating that the water flow is from bore 13 to bore 30, then additional $CO_2$ must be acquired by the water during this travel to satisfy the observed $CO_2/H_2O$ ratio. As $^{14}CO_2$ cannot be added underground, the additional $CO_2$ must be "old" and thus the $^{14}C/^{12}C$ ratio of the $CO_2$ in bore 30 would be $(17/170 \times 1{\cdot}4\%)$, i.e., $0{\cdot}14\%$. As the observed value for bore 30 is $0{\cdot}50\%$ it is apparent that water is not moving from bore 13 to bore 30.

If, as is more likely, the movement of water is from bore 30 to 13 then two distinct features are apparent. Firstly, there must be a loss of $CO_2$ from the water to reduce the $CO_2/H_2O$ ratio to that observed and secondly, there must be an addition of more young groundwater in order to raise the $^{14}C/^{12}C$ ratio to that observed for bore 13. Neither of these postulates is in disagreement with present theories for the Wairakei thermal area, for the loss of gas could explain the high $CO_2/H_2O$ ratios observed in fumaroles such as 712 and 612 and the addition of cold groundwater could explain the lower temperature of the water at bore 13.

### *Comparison of Fumaroles and Bores*

In Fig. 2 there is seen a bias toward higher values of the concentrat ing factor for fumaroles compared with bores. Fumaroles are almost invariably situated on slightly higher ground than boiling pools—but nevertheless very close to them—thus, in all fumaroles the steam may be evaporated from water which later appears in the adjacent pools. In general, $CO_2$ will follow the steam rather than the water, and the above-mentioned bias may be due to this effect. Particular features of the observed data will now be dealt with in more detail.

In Table 1, the vague grouping of bores and of fumaroles in the $CO_2/H_2O$ column becomes definite in the $^{14}C/H_2O$ column.

In the $^{14}C/^{12}C$ column there is a distinct grouping into two classes; Bore 30 and fumaroles 612 and 712, with approximately the same ratio (average $0{\cdot}6\%$ atmospheric) and bore 13 and fumarole 712A, with approximately the same ratio (average $1{\cdot}6\%$ atmospheric).

Not much can be stated about the equality of the $^{14}C/^{12}C$ ratio in bore 30 and fumaroles 612 and 712, except that they could be drawing $CO_2$ from a common source.

The fact that the $^{14}C/^{12}C$ ratios for 13 and 712A are equal and different from the $^{14}C/^{12}C$ ratio for 712, is curious. Inspection of a geological map of the area prepared by Mr G. W. Grindley (Report N94) (pers. comm.) shows several parallel faults. One passes through 712A, the next through 712, and the next again is almost certainly intersected by bore 13. Again, according to Grindley, the shallow flow of groundwater in the area is in the general direction from fumaroles 712 and 712A to bore 13. A possible explanation is that most of the $^{14}C$ is carried along the faults by the shallow groundwater, in a time very much less than the half-life of $^{14}C$ (5,570 years), while "old" $CO_2$ comes up the fault through 712, a fraction leaking into the faults on either side. As the faults on either side of 72 are about the same distance from the fault through 712, so the fraction of old $CO_2$ leaking across might be expected to be the same in both. Thus, the dilution of young $CO_2$ in the groundwater in the two side faults would be about the same, and be less than the dilution in the middle fault, making the $^{14}C/^{12}C$ ratios in 13 and 712A equal, and higher than the $^{14}C/^{12}C$ ratio in 712.

### *Effect of Pumped Cold Water*

During drilling of bores in the field, cold water (containing $^{14}C$) is of course being pumped into the steam-producing area, and the effect of this on the $^{14}C/^{12}C$ ratios of $CO_2$ in the bore discharges must be considered. The cooling water is obtained from a nearby stream, and its likely $CO_2$ content is 10 mol./$10^6$ mol. $H_2O$ (Goldschmidtt, 1954). The maximum average rate of pumping of cold water into the field is 100 gal./min. (J. H. Smith, pers. comm.) so that the maximum rate of pumping in of young $CO_2$ is $4 \times 10^{-3}$ mol./sec. The output of water and steam from bore 30 is 1000 gal./min., so that the output of $CO_2$ is 0·8 mol./sec. Assuming the worst, i.e. that all the young $CO_2$ emerges at bore 30, then the maximum possible $^{14}C/^{12}C$ ratio due to contamination with cooling water is 0·5% atmospheric. However, as the output of bore 30 is only 10% of the field, it is not likely that all the young $CO_2$ pumped down during drilling would emerge from bore 30—thus, the effect of this young $CO_2$ on observed $^{14}C^{12}C$ ratios is probably negligible.

## Conclusions

$^{14}C$ has been detected in all samples of $CO_2$ from bores and fumaroles in the Wairaeki area that have so far been analysed.

The main factors affecting the concentration of $^{14}C$ emerging with hot water in thermal areas are: the decay of $^{14}C$, the addition (underground) of $^{14}C$-free $CO_2$, the separation of $CO_2$ and $H_2O$, and the variation of "young" $CO_2$ concentration in surface water. The present measurements from five locations at Wairakei are not capable of resolving completely the effects of the above factors. They do show, however, that surface water can penetrate to a depth of at least 1,500 ft in less than 40,000 years. Also, at the five locations measured, the water can-

not have been depleted in $CO_2$ at any stage by more than a factor of 300, or enriched by more than a factor of 4,000.

The ultimate usefulness of $^{14}C$ measurements in the thermal areas will be more nearly attained when they are linked with other available data—especially with tritium ages of the water.

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## REFERENCES

BRINKMANN, R.; MUNNICH, K. O.; VOGEL, J. C., 1959: $^{14}C$ Altersbestimmung von Grundwasser. *Naturwissenschaften 46* : 1-2.

BROECKER, W. S.; WALTON, A., in press: The Geochemistry of $^{14}C$ in the Fresh Water Systems of the Great Basin. *Geochim. et cosmoch. Acta.*

BUTTLAR, H. V.; LIBBY, W. F., 1955: Natural Distributon of Cosmic Ray produced Tritium II. *J. Inorg. Nuclear Chem. 1* : 75-91.

CRAIG, H.; BOATO, G.; WHITE, D. E., 1955: Isotopic Geochemistry of Thermal Waters. *In* Nuclear Processes in Geologic Setting: 29-38. *Nat. Acad. Sci.-Nat. Res. Coun. Publ. 400*, Washington, D.C.

GRANGE, L. I., 1955 (Compiler): Geothermal Power for New Zealand. *N.Z. Dep. sci. industr. Res. Bull. 117.*

FERGUSSON, G. J., 1955: Radiocarbon Dating System. *Nucleonics 13,* 1 : 18-23.

GOLDSCHMIDTT, V. M., 1954. "Geochemistry", p. 349, Clarendon Press Oxford.

HUTCHINSON, G. E., 1954: "The Earth as a Planet". Ed. by G. Kuiper, University of Chicago Press, Chicago. pp. 371-433.

KAUFMAN, S.; LIBBY, W. F., 1954: The Natural Distribution of Tritium. *Phys. Rev. 93* : 1337.

LIBBY, W. F., 1955: "Radiocarbon Dating", 2nd edit. University of Chicago Press, Chicago.

STUDT, F. E., 1957: Wairakei Hydrothermal System and the Influence of Ground Water. *N.Z. J. Sci. Tech. 38B* : 595-622.

SMITH, J. H., 1958. Production and Utilization of Geothermal Steam. *N.Z. Engng. 13* : 354-75.

WILSON, S. H., 1955: *in* Grange, L. I. (compiler). Geothermal Power for New Zealand. *N.Z. Dep. sci. industr. Res. Bull. 117.*

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